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MORE SOFT-BODIED ANIMALS AND ALGAE
FROM THE MIDDLE CAMBRIAN OF UTAH
AND BRITISH COLUMBIA¹

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Abstract—Remains of noncalcareous algae and soft-bodied metazoans from Middle Cambrian strata of Utah (Spence, Wheeler, and Marjum formations) and British Columbia (Stephen Formation) provide further evidence for the wide geographic distribution and long stratigraphic ranges of many Burgess shale taxa. Among the algae, *Marpolia spissa*, here described from the Spence Shale and questionably from the Wheeler Formation, is referred to the oscillatoracean Cyanobacteria. *Margaretia dorus* is reported from the Spence and Wheeler formations and is interpreted as a caulerpalean Chlorophyta. *M. ramosa* and *M. stosei* from Pennsylvania and *Aldanophyton antiquissimum* from eastern Siberia are suppressed as junior synonyms of *M. dorus*. *Acinocricus stichus* n. gen. and n. sp. from the Spence Shale bears multiple whorls of spines at regular nodes on an elongate axis and is questionably assigned to the Chlorophyta. New material of *Yuknessia simplex*, which is also questionably assigned to the Chlorophyta, is described from the Spence, Wheeler, and Marjum formations. Tubicolous fossils from the Stephen Formation are reassigned to *Cambrorhytium* n. gen. with two species, *C. major* and *C. fragilis*. *C. major* is also illustrated from the Marjum Formation. New occurrences of *Selkirkia* sp. cf. *S. columbia* from the Spence Shale may extend geographic and stratigraphic ranges of this tubicolous priapulid worm. *Naraoia compacta* is reported for the first time from the Wheeler Formation, thereby adding to the observed distribution of this unusual trilobite. The arthropod *Ennomocaris spinosa* n. gen. and n. sp. from the Wheeler Formation is remarkable for its large size and prominent spines. The arthropod *Utahcaris orion* n. gen. and n. sp. from the Spence Shale has an elongate

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body with cephalic shield and telson of subequal size. One undetermined arthropod from the Spence Shale resembles *Emeraldella* and *Leancoilia*. Another undetermined arthropod from the Marjum Formation resembles *Actaeus* and *Alalcomenaeus*. Although fragmentary, the first appendages of *Anomalocaris nathorsti* to be discovered in Utah are described from the Spence and Wheeler formations. New discoveries in Utah of isolated sclerites of *Wiwaxia* sp. cf. *W. corrugata* and compressions of the medusiform *Eldonia ludwigi*, both of uncertain systematic position, provide the first records of these taxa from beyond the Burgess shale of British Columbia. Undetermined worms are described from the Wheeler Formation. Large coprolites in the Spence Shale are indicative of a predator or scavenger that may have been larger than any animal previously reported from Cambrian rocks.

EVOLUTIONARY AND ECOLOGICAL insights provided by the Burgess shale biota from the Middle Cambrian of British Columbia (e.g., Conway Morris, 1985a, 1986; Conway Morris and Whittington, 1985; Whittington, 1985) are becoming more widely appreciated, especially as they pertain to the diversification of early metazoans. So long as the Burgess shale biota remained an isolated occurrence, however, its wider relevance to Cambrian studies was inevitably somewhat elusive. The discovery in other Cambrian localities of soft-bodied fossils that are directly comparable to those from the Burgess shale is, therefore, of particular significance in demonstrating the wide distribution of this biota. Many sites are now known from around the Laurentian craton, which during the Cambrian Period appears to have occupied an equatorial location isolated from other major cratons (Smith, Hurley, and Briden, 1981; Zonenshain, Kuzmin, and Kononov, 1985). At present this distribution is defined by occurrences as widespread as California, Utah, Idaho, British Columbia, North Greenland, and Pennsylvania (Conway Morris, 1985b; Robison, 1986; Conway Morris and others, 1987).

Here we report occurrences of new taxa of algae and arthropods from Utah that enlarge our knowledge of Cambrian diversity. Notes are also given on a variety of forms already known from the Burgess shale and, less commonly, other Laurentian localities. We reiterate and extend the conclusions reached in a series of related papers (Conway Morris and Robison, 1982, 1986; Briggs and Robison, 1984; Robison, 1984b, 1985, 1986) that a biota of Burgess shale type was widespread in open-

shelf environments of the Lower and Middle Cambrian (see also Conway Morris, 1985b; Conway Morris and others, 1987). Moreover, these studies suggest that the shelly assemblages normally available to paleontologists represent only a small fraction of the original community, and if taken in isolation are an insecure foundation for paleoecologic analyses.

Some of the wider implications of the continuing discoveries of biota of Burgess shale type will be discussed elsewhere, and only brief comments are given here. In terms of geographic distribution not only is the circum-Laurentian pattern now clear, but recent discoveries in the Lower Cambrian of Yunnan Province, southwestern China (Zhang and Hou, 1985; Hou, 1987a, b, c; Sun and Hou, 1987a, b; Hou and Sun, 1988; see also Mansuy, 1912; P'an, 1957; Jiang, 1982), are of special importance given the postulated paleogeographic separation between the Laurentian and Chinese cratons. This distribution, combined with a tendency for biotas of Burgess shale type to occur in deep-water lithofacies, suggests that migration between at least these cratons could have occurred via deep waters of the intervening ocean (for similar postulate to explain affinities in Upper Cambrian trilobites, see Taylor and Cook, 1976). It seems likely that further exploration in appropriate facies will extend the distribution of biotas of Burgess shale type.

Reports of Burgess shale taxa from the Lower Cambrian of southwestern China (Zhang and Hou, 1985) and North Greenland (Conway Morris and others, 1987) also complement previous data on occurrences in this stratigraphic interval (e.g., Kinzers Formation

of Pennsylvania, Latham Shale of California) and indicate striking longevities in a number of genera. Taken together, these long ranges indicate a strong evolutionary conservatism in this biota.

The increases in geographic distributions and stratigraphic ranges reported here are more modest. Nevertheless, such data are important because of the wider contexts of the history of this distinctive biota, including its origin in the earliest Cambrian and its ultimate fate in the deeper waters of the Paleozoic oceans.

Stratigraphy.—The fossils described here are from four formations. Fossils from west-central Utah are from either the Wheeler or Marjum formations of late Middle Cambrian age (*Ptychagnostus atavus* and *P. punctuosus* interval-zones of Robison, 1984a). Fossils from northern Utah are all from the Spence Shale of early Middle Cambrian age (*Peronopsis bonnerensis* Assemblage-zone or, with reference to polymeroid trilobites, *Glossopleura* Assemblage-zone of Robison, 1976). The fossils from British Columbia are all from the Stephen Formation, including the informal *Ogygopsis* shale and Burgess shale localities, and are of early Middle Cambrian age. Fauna of the *Ogygopsis* shale correlates with that of the *Glossopleura* Zone and the fauna of the Burgess shale contains *Ptychagnostus praecurrens*, which is indicative of the *P. praecurrens* Interval-zone (Robison, 1984a).

Localities.—Utah localities referred to in this paper by three-digit numbers are described in files of The University of Kansas Museum of Invertebrate Paleontology. All of these localities are in either the Wellsville Mountains of Box Elder County, northern Utah, or the House Range or Drum Mountains of Millard County, west-central Utah. Topographic names mentioned from the Wellsville Mountains are shown on the Brigham City quadrangle map (U.S. Geological Survey, 1955, 7.5-minute series), and those from the House Range are on the Marjum Pass quadrangle map (U.S. Geological Survey, 1972, 7.5-minute series).

Repositories.—All described specimens are deposited with either the Geological Survey of Canada (GSC), The University of Kansas Museum of Invertebrate Paleontology (KUMIP), Lawrence, or the U.S. National Museum of Natural History (USNM), Washington, D.C.

Acknowledgments.—Most of the taxa de-

scribed here are represented by rare specimens that have been generously contributed by several individuals. Special gratitude is due Lloyd and Val Gunther for numerous and invaluable donations. Important specimens have also been provided by R. A. Cooper, B. F. Dattilo, Frieda Gunther, Glade Gunther, the late Metta Gunther, R. L. Harris, G. F. Melloy, Nancy Meyers, Robert Meyers, and G. F. Rockers. Access to and loan of material at the U.S. National Museum of Natural History was efficiently arranged by F. J. Collier. SCM thanks Sandra Last for typing manuscript, Sheila Ripper for drafting some figures, and Ken Harvey and David Bursill for photographic assistance; travel was supported in part by the Royal Society and the Cowper-Reed Fund. He is also grateful to colleagues at the Nanjing Institute of Geology and Palaeontology, especially Sun Wei-guo, Hou Xian-guang, Zhang Wen-tang, and Chen Jun-yuan, for permission to examine material from Chenjiang, China, as part of the Royal Society-C.A.S.T. Exchange Scheme. RAR had photographic assistance from Byron Wiley and was supported by National Science Foundation grants EAR-8519324 and EAR-8720333. Constructive reviews were given by L. E. Babcock, D. E. G. Briggs, and C. G. Maples. This is Cambridge Earth Sciences Publication 1084.

SYSTEMATIC PALEONTOLOGY

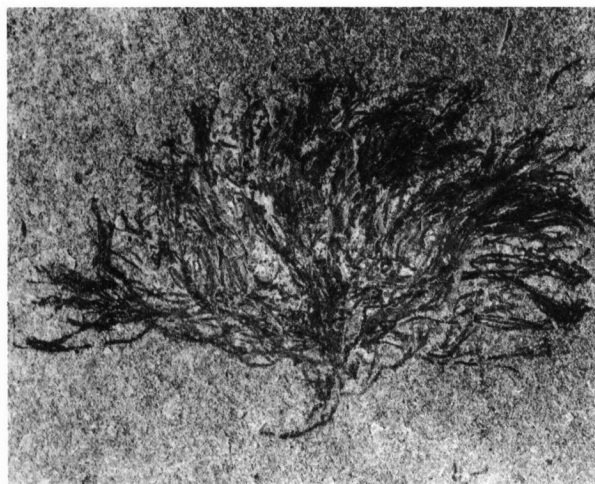
Kingdom MONERA
Division CYANOBACTERIA
Class MYXOPHYCEAE
Order HORMOGONALES
Family OSCILLATORIACEA

Genus MARPOLIA Walcott, 1919

Remarks.—Widely different taxonomic affinities have been proposed for *Marpolia*. Walcott (1919:233–234) originally assigned the genus to the blue-green algae (order Hormogoneae, family Nostocaceae). From a study using transfer peels, Walton (1923) provisionally reassigned *Marpolia* to the Protophyceae, a group of “primitive algae whose relationships to the modern phyla are unknown or uncertain.” Without discussion, Johnson (1966:24–25) considered *Marpolia* to be a red alga (phylum Rhodophycophyta) of uncertain family position. From a study of many new specimens, Satter-

thwait (1976:55–62), using parloidian transfer peels, was the first to demonstrate the cellular organization of *M. spissa* Walcott, 1919, the type species of *Marpolia* (see Fig. 2). Based on avail-

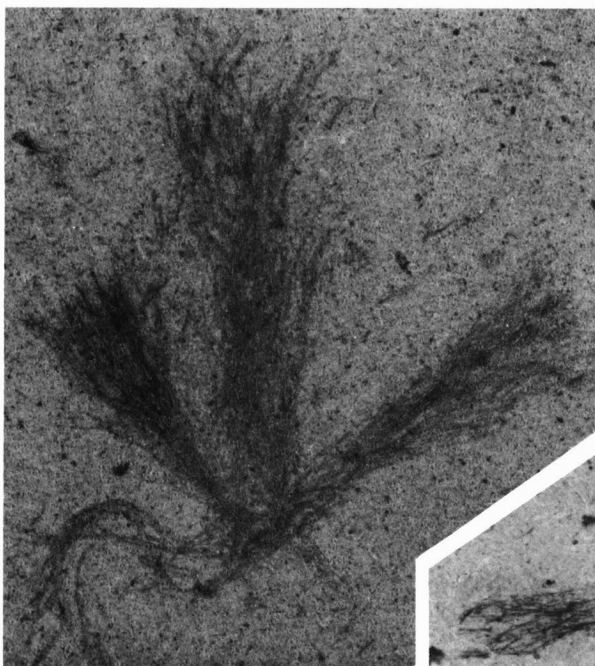
able information, she concluded that representatives of the genus are cyanophytes of the family Oscillatoriaceae. We concur with that assignment.



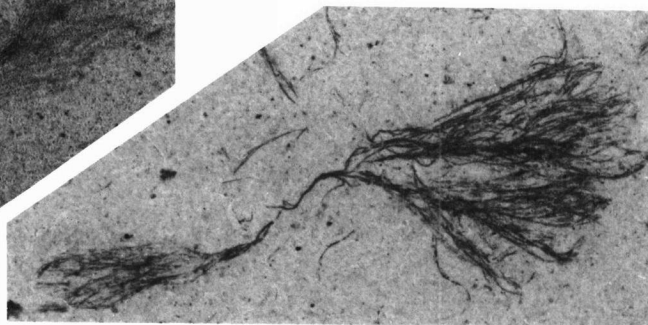
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Fig. 1. *Marpolia spissa* Walcott.—1–3. Thalli from upper Spence Shale, locality 781, Wellsville Mountains; 1, KUMIP 111765, $\times 2.5$; 2, KUMIP 111764, $\times 2.0$; 3, KUMIP 127799, $\times 2.0$.—4. ?*M. spissa* Walcott; thallus from upper Wheeler Formation, locality 115, House Range; KUMIP 204372.

A close relationship between bacteria and the blue-green algae is now widely accepted. Pending achievement of a clear consensus on the higher classification of these organisms, we provisionally follow that of Humm and Wicks (1980).

MARPOLIA SPISSA Walcott, 1919

Figures 1, 2

Marpolia spissa WALCOTT, 1919, p. 234, pl. 52, figs. 1, 1a-b; WALTON, 1923, p. 59-62, pl. 5; JOHNSON, 1966, p. 24-25, pl. 7, figs. 1-3; GUNTHER and GUNTHER, 1981, pl. 67B; CONWAY MORRIS and WHITTINGTON, 1985, fig. 4; WHITTINGTON, 1985, fig. 4.2.; BABCOCK and ROBISON, 1988, fig. 1,1.

Lectotype.—Thallus, USNM 35403, illustrated by Walcott, 1919, pl. 52, fig. 1; selected here.

New material.—Ten more or less complete thalli collected by Lloyd and Val Gunther from the Spence Shale, and many dissociated filaments and fragments. One questionably assigned specimen was collected by Robert Harris from the Wheeler Formation.

Emended diagnosis.—Thallus small; commonly between 2 and 3 cm high, ranging to about 5 cm. Filaments numerous, branching basally at low angles to form a dense tuft. Most filaments composed of an outer, thick, organic sheath and an inner trichome of uniserial cells. Filament width ranges from 20 to 60 μ and averages about 40 μ . Rarely, two to four trichomes occupy a single sheath. Rare trichomes may be naked. Cells of trichome discoidal, length ranging from 2 to 4 μ , width from 2 to 10 μ ; heterocysts absent. Terminal cells of trichome unknown.

Discussion.—The emended diagnosis of *M. spissa* is partly based on an unpublished description by Satterthwait (1976). New specimens from Middle Cambrian strata in Utah add little morphological information about the species, but they do increase knowledge of its distribution.

Satterthwait (1976:55) noted that *M. spissa* is the most abundant megascopic alga collected from the Burgess shale quarry in the Stephen Formation of British Columbia. Data assembled by one of us (SCM) indicates that in collections of the U.S. National Museum of

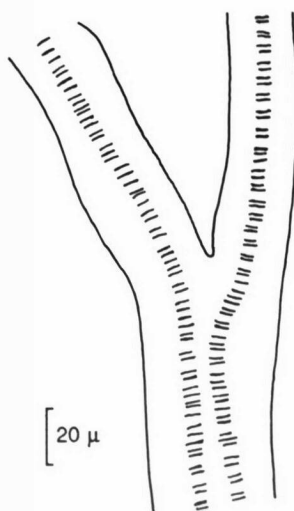


Fig. 2. Diagrammatic reconstruction of cellular organization in *Marpolia spissa* Walcott (after Satterthwait, 1976).

Natural History this alga is on about 180 rock slabs, often in profusion. In the Stephen Formation near the Burgess shale quarry, the number of localities with *Marpolia* is second only to that with *Margaretia* (Collins, Briggs, and Conway Morris, 1983, table 1).

A few tufts of *M. spissa* have been collected from the Spence Shale in Utah. More commonly, dissociated and broken filaments are preserved on some bedding surfaces (e.g., Babcock and Robison, 1988, fig. 1,1), but these are easily overlooked and may be difficult to identify. Thus, the reported occurrences of *M. spissa* are not likely to be indicative of its original distribution or abundance in the Middle Cambrian biota of North America.

A single large mass of filaments (Fig. 1,4) from the Wheeler Formation is questionably assigned to *M. spissa*. The filaments are shorter, finer, and more numerous than is usual for representatives of the species in older strata.

Based on observed distributions of modern algal morphotypes and a close similarity between *M. spissa* and the extant *Porphyrosiphon kurizii*, Satterthwait (1976:61, 64) suggested that *M. spissa* may have lived in habitats extending from the littoral zone to depths as great as 20 m. Nevertheless, the specimens of *M. spissa* from Utah show no evidence of substrate attachment at the time of burial and the pos-

sibility of their transport by currents into deeper water, especially during storm events, should not be ruled out.

Occurrence.—*M. spissa* is unquestionably known from only the lower Middle Cambrian of western North America. Type specimens from the Burgess shale of British Columbia are from the *Ptychagnostus praecurrens* Zone. New material from locality 781 in the Spence Shale of Utah is from the underlying *Peronopsis bonnerensis* Zone. A questionably assigned specimen from locality 115 in the upper Wheeler Formation of Utah is from the *Ptychagnostus atavus* Zone of middle Middle Cambrian age.

Kingdom Protocista
Division CHLOROPHYTA
Class CHLOROPHYCEAE
Order CAULERPALES
Family CAULERPACEAE

Genus MARGARETIA Walcott, 1931

Margaretia WALCOTT, 1931, p. 2; HANTZSCHEL, 1962, p. W225; 1975, p. W151.

Aldanophyton KRISHTOFOVICH, 1953, 1378–1379.

Type species.—*Margaretia dorus* Walcott, 1931, p. 2–3, pl. 1, figs. 1–6; by original designation.

Emended diagnosis.—Thallus large, tubular, nonsymmetrical, and noncalcareous; differentiated into prostrate rhizome and multiple, erect, branching axes. Rhizomic surface having irregular undulations and widely spaced axial attachment sites. Axis characteristically papillate. Axial branching commonly dichotomous or rarely trichotomous.

Discussion.—The genus *Margaretia* was established for fossils from the Burgess shale by posthumous publication of preliminary notes by C. D. Walcott. A similarity to living algae was mentioned (Walcott, 1931:3), together with a comment that “the resemblance is only general.” An explanatory note by C. E. Resser (in Walcott, 1931:2) stated that Walcott’s latest opinion was that *Margaretia* “might really be an Alcyonarian.” That opinion seemingly influenced Resser and Howell (1938), who questionably assigned two new species of *Margaretia*, from the Kinzers Formation of Early Cambrian age, to the Coelenterata. Häntzschel (1962, 1975) subsequently included *Margaretia* with genera of doubtful or uncertain classificatory

status and noted only that it had been compared with algae and alcyonarians. In an unpublished dissertation, Satterthwait (1976: 42–54) reviewed the morphology of *Margaretia* and concluded that it is a green alga with close similarity to modern *Caulerpa*. After further study, we agree with Satterthwait’s conclusion. In fact, specimens of *Margaretia* show no characters of external anatomy that differ significantly from those of some *Caulerpa*, which is noted for its great variety of shapes (Bold and Wynne, 1985:229). Nevertheless, in the absence of information about such characters as cytology, cell-wall chemistry, and life history, we provisionally retain *Margaretia* as a separate genus.

M. dorus was designated by Walcott (1931:2) as the type species of *Margaretia*, and it was the only species that he assigned to the genus. Three other species, *M. angustata* Resser, 1938, *M. ramosa* Resser and Howell, 1938, and *M. stosei* Resser and Howell, 1938, were subsequently described. Specimens of *M. ramosa* and *M. stosei* were distinguished by Resser and Howell (1938) from those of *M. dorus* by differences in axial width and by the presence of smaller papillae. Also, as emphasized by the name, *M. ramosa* was described as being ramose. Since all of these differences fall within the ranges of character variation observed in single populations of *M. dorus*, we here consider *M. ramosa* and *M. stosei* to be subjective junior synonyms of *M. dorus*. This variation also falls within ranges observed in many species of modern marine algae, which have long been known for their phenotypic plasticity (Dixon, 1970). The holotype of *M. angustata* is difficult to assess; it may represent *Margaretia* or it may be a tiny, pellet-filled burrow. *Aldanophyton* Krishtofovich, 1953, from the middle Middle Cambrian of eastern Siberia was described as a lycopod-like plant. Its gross morphology was compared with that of several primitive vascular plants but was said by Krishtofovich to have nothing in common with any Cambrian alga. Nevertheless, all described and illustrated characters of its single species, *A. antiquissimum* Krishtofovich, 1953, closely resemble those of *M. dorus*. Hence, we consider these species to be synonyms and we consider *Aldanophyton* to be a junior synonym of *Margaretia*.

As revised, *Margaretia* unequivocally includes one species, *M. dorus*.

The large size, tubular (siphonous) struc-

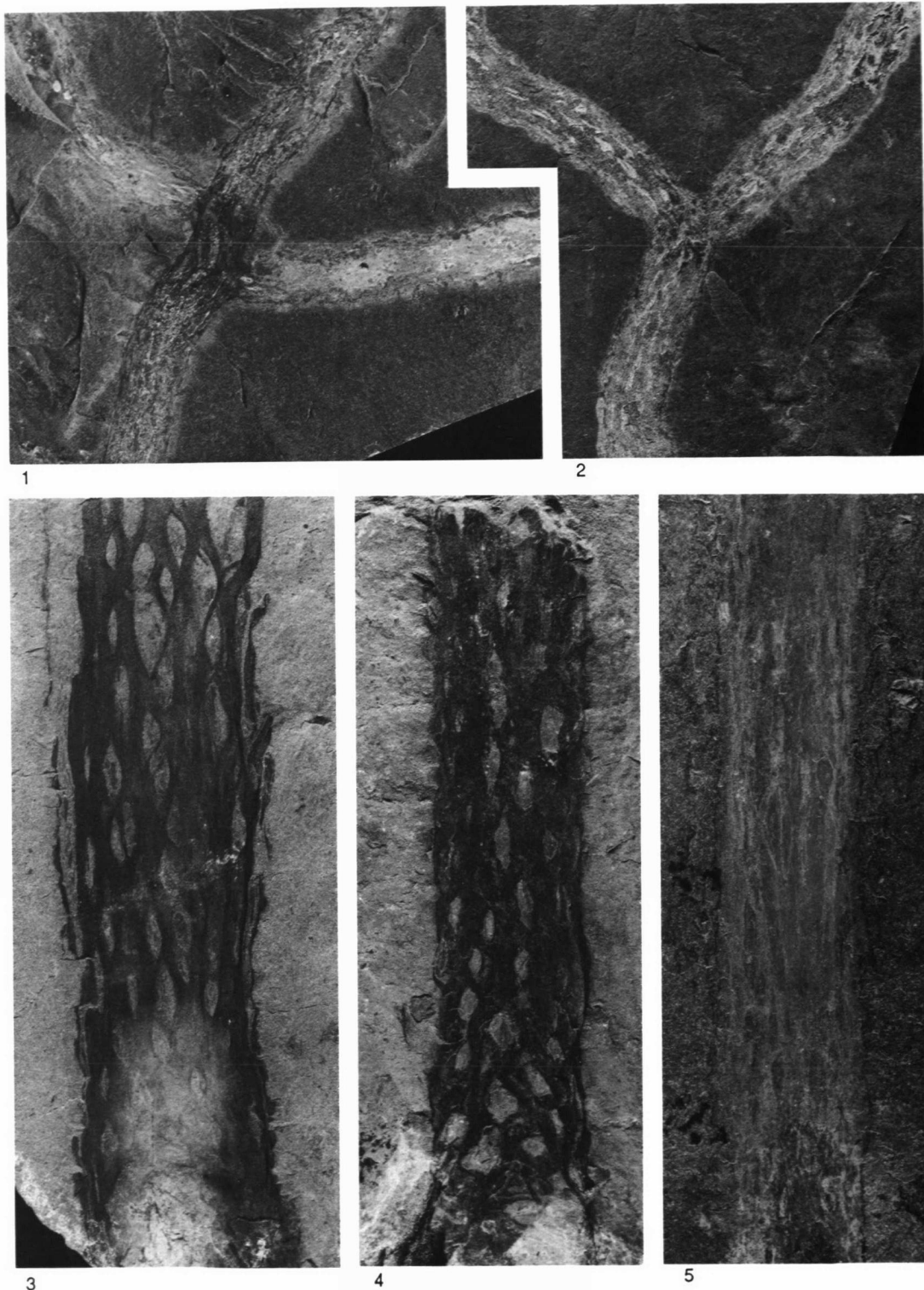


Fig. 3. *Margaretia dorus* Walcott. —1, 2. Axial fragments showing trichotomous and dichotomous branching, respectively; both from upper Wheeler Formation, locality 116; KUMIP 204373 and 204374, both $\times 1$. —3, 4. Axial compressions with many almond-shaped holes where papillae have been sheared off along parting surfaces in lime mudstone (3, 4 same as Fig. 4, 1a, b); both from upper Wheeler Formation, locality 115; KUMIP 204375 and 127810, $\times 1.6$ and 1.2 , respectively. —5. Axial compression in noncalcareous clay shale from lower Spence Shale, locality 101; KUMIP 127793, $\times 1$.

ture, differentiation into prostrate rhizomic and erect multiaxial parts, and lack of calcification indicate that *Margaretia* is a chlorophyte assignable to the order Caulerpales and family Caulerpacae (compare Bold and Wynne, 1985:216–217). Synonymous order names are Siphonales and Bryopsidales (Hillis-Colinvaux, 1984:289). Among modern siphonous algae, the thalli are coenocytic (i.e., multinucleate and without cross walls) and essentially one-celled (Prescott, 1968:110). Studies of peels and transfers have produced no evidence of cellular structure in representatives of *Margaretia* (Satterthwait, 1976:43; also see Krishtofovich, 1953:1378), which accords with a coenocytic condition.

Caulerpa and closely related modern genera are mostly restricted to tropical or subtropical marine environments (Hillis-Colinvaux, 1984:285). Cambrian paleogeographic reconstructions (e.g., Smith, Hurley, and Briden, 1981) and paleoecologic information indicate that *Margaretia* also is known only from marine localities that were tropical or subtropical. The largest collections of *Margaretia* are from British Columbia and Utah, which were probably near the Cambrian equator.

MARGARETIA DORUS Walcott, 1931

Figures 3, 4

Margaretia dorus WALCOTT, 1931, p. 2–3, pl. 1, figs. 1–6; HÄNTZSCHEL, 1962, fig. 139.6; 1975, fig. 91.1; GUNTHER and GUNTHER, 1981, pl. 67C.

Margaretia stosei RESSER and HOWELL, 1938, p. 211, pl. 1, figs. 9–11.

Margaretia ramosa RESSER and HOWELL, 1938, p. 211, pl. 2, fig. 1.

Aldanophyton antiquissimum KRISHTOFOVICH, 1953, p. 1378–1379, pl. 1, figs. 1–5; ANDREWS, 1961, p. 47–50.

New material.—More than 80 axial fragments and a few rhizomic fragments, all compressed in matrix that varies in composition from noncalcareous clay shale to lime mudstone. Many of these specimens were collected by Lloyd Gunther, Val Gunther, and George Melloy.

Emended diagnosis.—As for genus.

Discussion.—*M. dorus* is an unusually large fossil alga. All available specimens are tubular fragments preserved as compressions. The ob-

served width of compressed axial fragments ranges from 6 to 23 mm and averages about 14 mm. These fragments range up to about 40 cm in length, but entire axes were probably much longer. The ends of some tubular fragments may be slightly flared, but otherwise the fragments probably underwent little lateral expansion during compression for reasons that were described by Briggs and Williams (1981).

Axial surfaces of *M. dorus* are covered with numerous distinctive papillae that are elongated in a direction parallel to the axial margin and that may be arranged in a roughly spiral pattern. If preservation is good, the outlines of laterally compressed papillae can be seen along axial margins (Figs. 3,3, 4,1a,b). When some matrix is separated, papillae that are more or less perpendicular to the parting surface are sheared off, leaving small, almond-shaped holes (Figs. 3,3–5, 4,4). It was probably such secondarily produced holes that led Walcott (1931:2) to incorrectly describe *M. dorus* as a “thin membranous perforated sheet.”

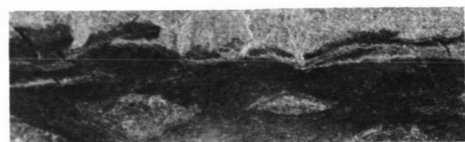
Limited evidence suggests that *M. dorus* may have reproduced both sexually and asexually, which is common among modern algae (Bold and Wynne, 1985:9). In some species of *Caulerpa*, numerous papillae develop on the erect axes and sometimes on the prostrate rhizome. At sexual maturity, gametes are passively released through ruptures in the papillae (Goldstein and Morrall, 1970). The papillae of *M. dorus* may have served a similar function. Common fragmentation of *M. dorus* also suggests that vegetative reproduction was a likely possibility. With this type of reproduction, cloning is achieved by a fragment developing into a new thallus by continuing growth (Bold and Wynne, 1985:10–11). Among modern algae, vegetative reproduction is common in *Caulerpa* and some species of *Halimeda* (Hillis-Colinvaux, 1984:284).

In general form and size, rhizomic fragments of *M. dorus* are quite similar to axial fragments. Differences are mainly in surface detail. The rhizomic surface is characterized by low and irregular undulations. Some bumps may resemble axial papillae, but there is neither regular elongation parallel to the rhizomic margin nor any hint of a spiral pattern. Large holes in the dorsal surfaces of two rhizomic fragments (arrows, Fig. 4,2,3) may be axial attachment

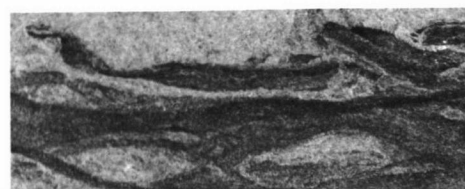
sites; however, an unbroken attachment of rhizome and axis has not been observed.

The collective characters of many fragments of *M. dorus* permit a much more complete

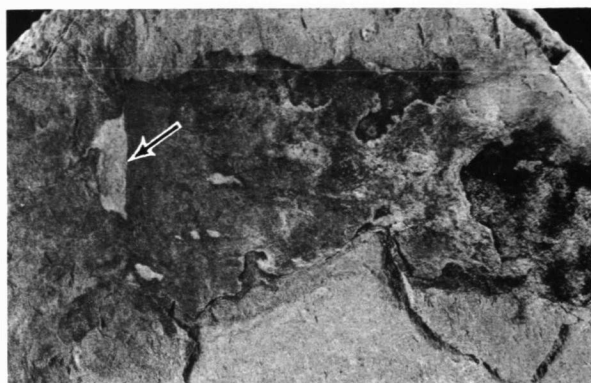
reconstruction of its general habit and gross anatomy than has previously been published. The tubular thallus evidently had a long rhizome that produced multiple, well-sepa-



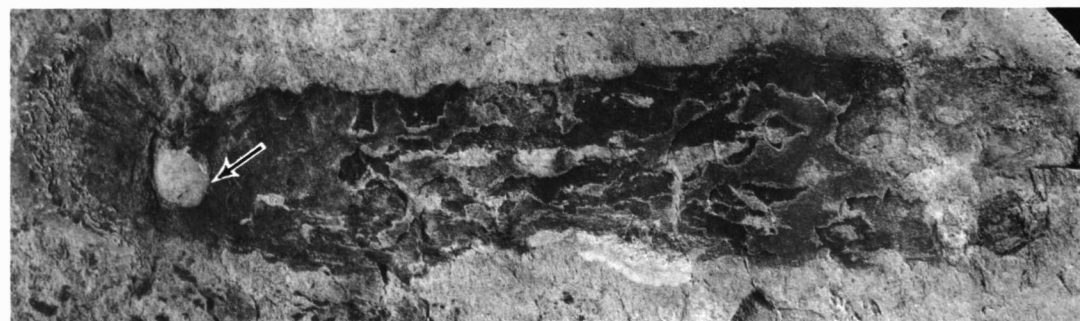
1a



1b



2



3

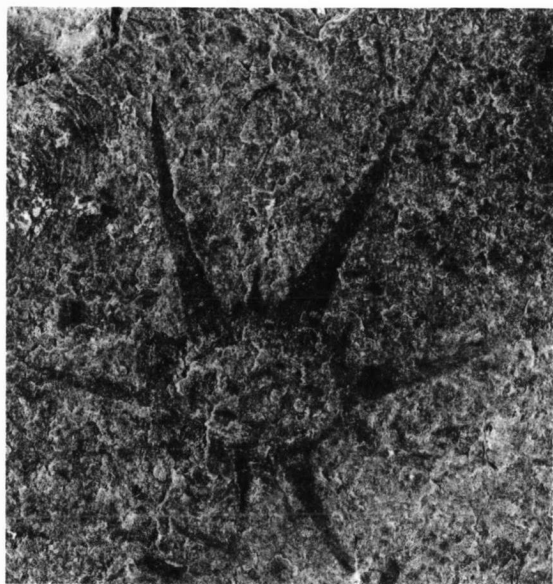


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Fig. 4. *Margaretia dorus* Walcott. —1a, b. Laterally compressed papillae along margins of axial compression (same as Fig. 3, 3), both $\times 5$. —2, 3. Rhizomic compressions with undulatory surfaces, each with a hole (arrows) that may represent a broken axial attachment site; both from upper Wheeler Formation, locality 115; KUMIP 204376 and 204377, $\times 2$ and 1.6, respectively. —4. Axial compression with mud filling to the left of transverse fracture; internal axial surface is exposed to the right of transverse fracture where filling has been removed; from upper Wheeler Formation, locality 115; KUMIP 147911, $\times 1.6$



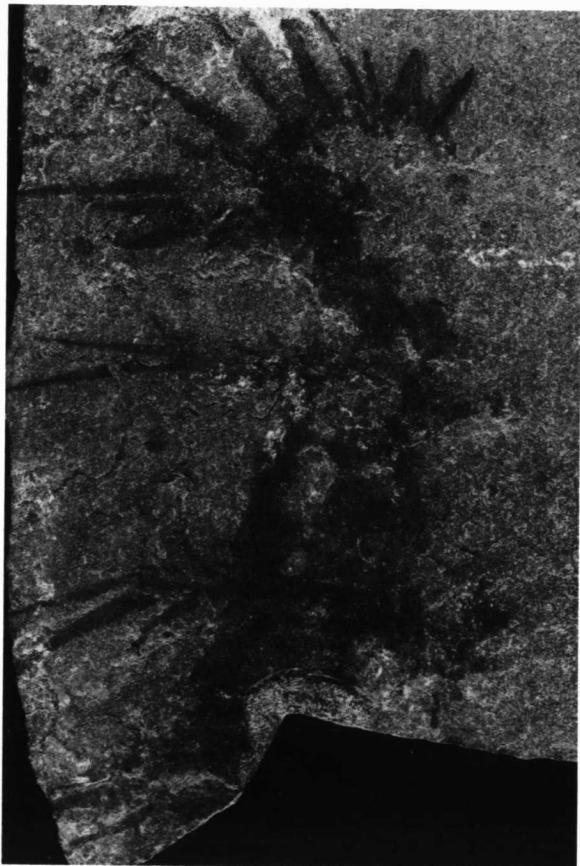
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Fig. 5. *Acinoericus stichus* n. gen. and n. sp. from the Spence Shale, Wellsville Mountains. —1. Incomplete whorl of spines from near top of formation, Miners Hollow, KUMIP 204354, $\times 3$. —2. Whorl of spines from middle of formation, Antimony Canyon; KUMIP 204355, $\times 3$. —3. Holotype from middle of formation, Miners Hollow, KUMIP 204353, $\times 1.5$. —4. Poorly preserved axial fragment with four spinose whorls; from middle of formation, Antimony Canyon; KUMIP 204356, $\times 3$.

rated, erect, photosynthetic axes. Dichotomous branching of axes is common, and axial surfaces are abundantly papillate. The thallus probably had a capacity for extensive and

essentially indeterminate growth like *Caulerpa* and *Halimeda* (compare Hillis-Colinvaux, 1984: 278). Also like *Caulerpa*, the principal growth axis of *M. dorus* is a rhizome, and the probable reproductive structures (papillae) are relatively unspecialized (compare Hillis-Colinvaux, 1984: 278–280). If the papillae of *M. dorus* functioned like those of some *Caulerpa*, the species probably was holocarpic, a condition in which the entire thallus is converted into a reproductive structure (Bold and Wynne, 1985:652). Holocarpy was considered by Hillis-Colinvaux (1984:284, fig. 2, table II) to be an important taxonomic character of the siphonous suborder Halimedineae, to which *Caulerpa* was assigned. Compared to modern green algae, *M. dorus* has a very large thallus. It, therefore, is of interest that the largest modern green algae belong to the suborder Halimedineae (Hillis-Colinvaux, 1984:275, fig. 2).

Occurrence.—*M. dorus* is known from Canada (British Columbia), the Soviet Union (eastern Siberia), and the United States (Pennsylvania, Utah). It is present in the following collections from Utah: 100 and 101 from the lower and middle Spence Shale of the Wellsville Mountains; 115, 116, 712, 799, and 803 from the upper Wheeler Formation of the Drum Mountains and House Range; and 811 from the middle Marjum Formation of the House Range. The species has an observed stratigraphic range from the upper Lower Cambrian (*Olenellus* Zone) to the upper Middle Cambrian (*Ptychagnostus punctuosus* Zone).

?Division CHLOROPHYTA
Class, order, family uncertain

ACINOCRICUS new genus

Etymology.—A combination of Greek *akaina*, thorn or spine, and *krikos*, ring; in reference to the prominent spinose circlets.

Type species.—*Acinocriscus stichus* n. sp. (Figs. 5–10).

Description.—Thallus consisting of long axis bearing prominent spinose whorls at more or less regular intervals. Elongate spines on each whorl separated by conspicuously shorter spines; arrangement may be bilaterally symmetrical. Whorls may house short branches with closely spaced spines, probably in whorls. Holdfast and distal termination not known.

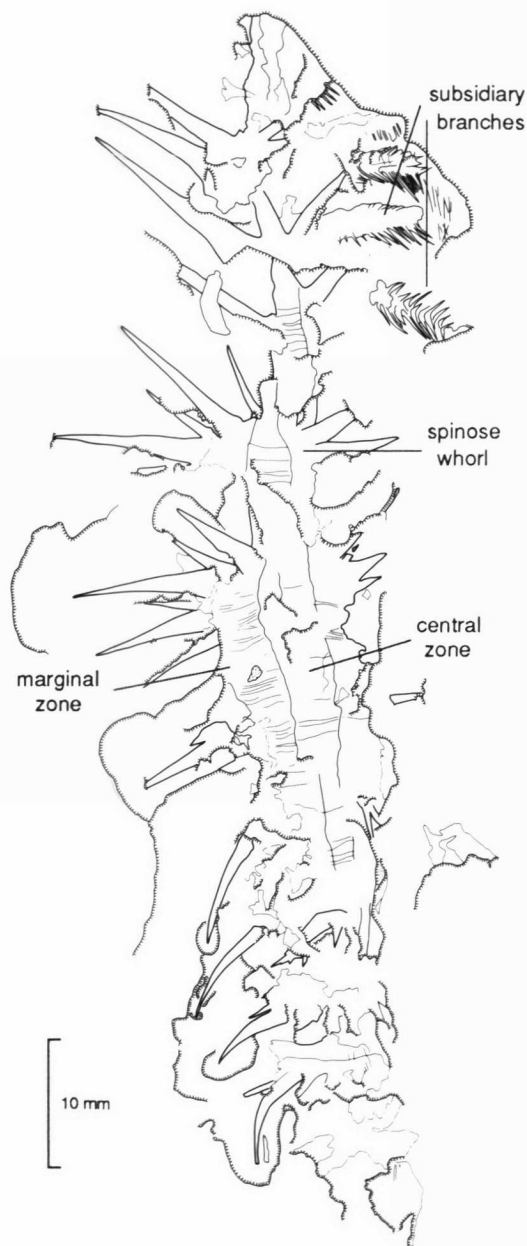


Fig. 6. *Acinocriscus stichus* n. gen. and n. sp., explanatory drawing of holotype, KUMIP 204353 (compare Figs. 5, 3, 9, 1).

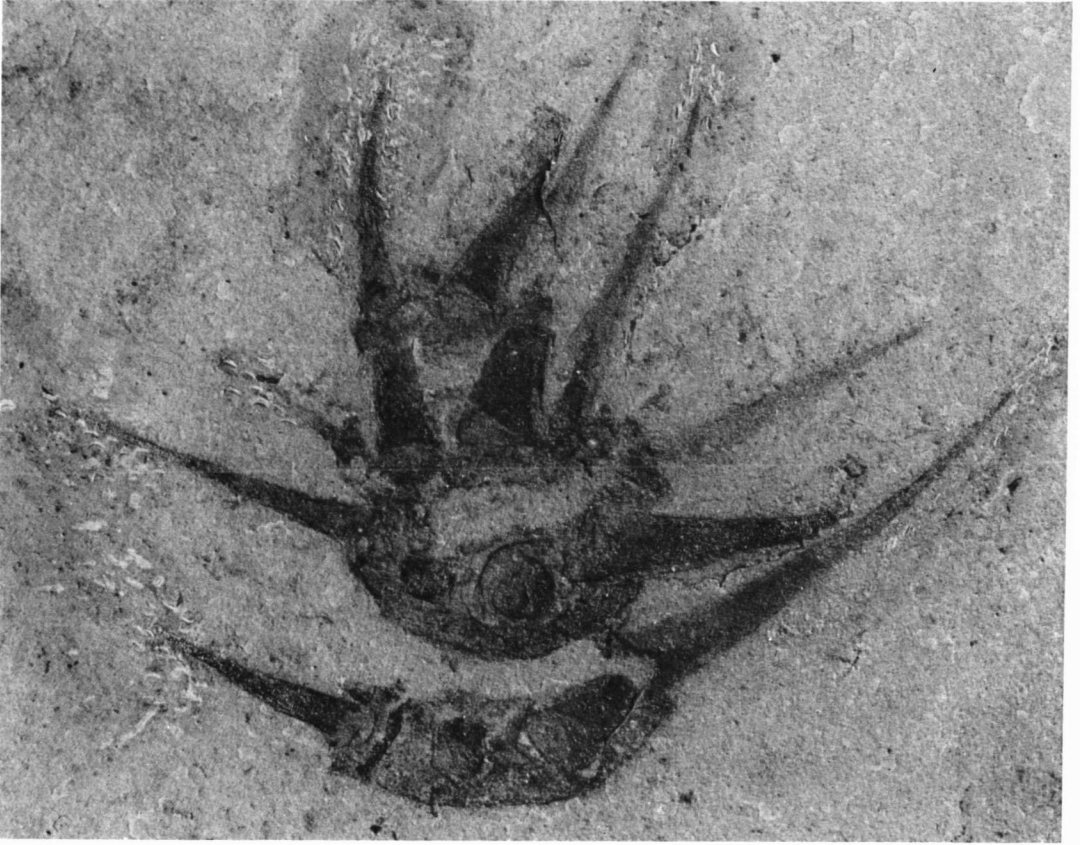


Fig. 7. *Acinocriscus stichus* n. gen. and n. sp.; whorls of spines with circular attachment areas; from about 3 m below top of Spence Shale in Miners Hollow, Wellsville Mountains; KUMIP 204776, $\times 4$.

Discussion.—An isolated whorl of this new taxon from the Spence Shale has been previously illustrated (Conway Morris and Robison, 1982, pl. 1, fig. 6; text-fig. 1C). From this single specimen we drew tentative comparisons with medusoid cnidarians, but noted (p. 120–121) that it “does not closely resemble other medusoids that have been described either from Cambrian or other strata” (see also Gunther and Gunther, 1981, pl. 58B; Briggs and Robison 1984:5).

ACINOCRISCUS STICHUS new species

Figures 5–10

Undetermined *Peytoia*-like medusoid GUNTHER and GUNTHER, 1981, pl. 58B.

Genus and species indeterminate CONWAY

MORRIS and ROBISON, 1982, p. 120–121, pl. 1, fig. 6; text-fig. 1C.

Etymology.—Greek *stichos*, row or line; referring to the multiple spinose whorls.

Holotype.—Incomplete thallus, KUMIP 204353 (Figs. 5, 3, 6, 9, 1), collected by Lloyd Gunther from the middle part of the Spence Shale in Miners Hollow, Wellsville Mountains, Utah. The specimen is compressed in hard, flaggy parting, pale-brown to medium dark-gray, noncalcareous mudshale.

Other material.—Four axial fragments with multiple whorls (KUMIP 204356, 204357, 204358, 204776) and at least 13 detached whorls. All are compressions from the Spence Shale, and all were collected by Lloyd and Val Gunther.

Description.—In only the holotype is the

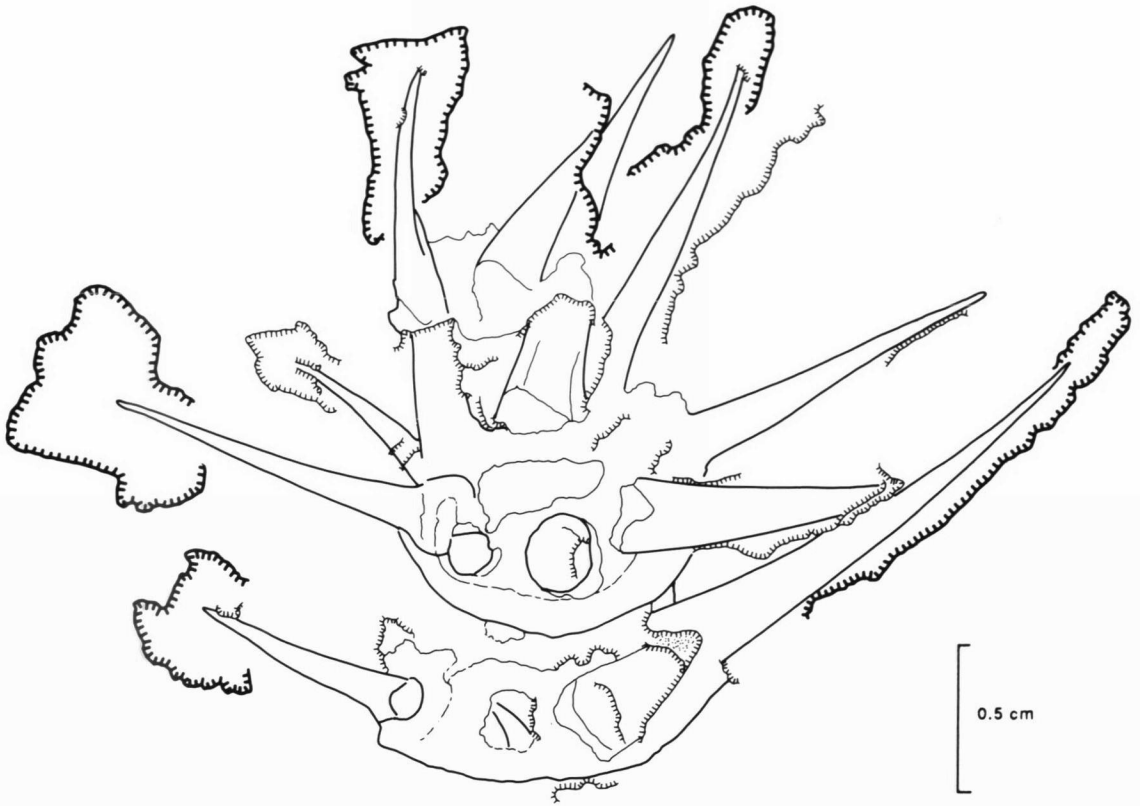


Fig. 8. *Acinocricus stichus* n. gen. and n. sp., explanatory drawing of KUMIP 204776 (compare Fig. 7).

thallus preserved in anything approaching completeness, with a broad axis bearing approximately 10 whorls of spines (Figs. 5,3, 6). Neither end is clearly preserved, and thus the nature of the basal attachment and distal termination is speculative. The axis in this specimen is about 97 mm long and 9.5 mm wide. The central zone of the axis forms a distinct unit that is divided by transverse structures, whereas the more marginal areas also bear faint striations. Three other axial fragments (Figs. 5,4, 7, 9,2) consist of multiple whorls, but in only one of these specimens are poorly preserved remains of the axis discernible (Fig. 5,4).

Most specimens are detached whorls of spines (Fig. 5,1,2), but their original arrangement can be seen in specimens with multiple whorls. In the holotype the whorls at either end point in opposite directions, whereas those in

the middle project more or less perpendicular to the axis. It is uncertain whether this variation in pointing direction of the whorls is original or due to postmortem processes. It is evident, however, that most and perhaps all whorls had their spines recurved so that their distal sections were subparallel to the stem. In another specimen (Fig. 9,2a,b), which evidently was buried at a steep angle to the bedding, four partially overlapping whorls can be distinguished, although the intervening axis is not clearly preserved. Finally, in the remaining semiarticulated specimen, two whorls and the trace of a third show a nested arrangement that probably reflects in part the angle of burial. Despite the well-preserved whorls, however, no clear trace of the axis remains (Figs. 7, 8).

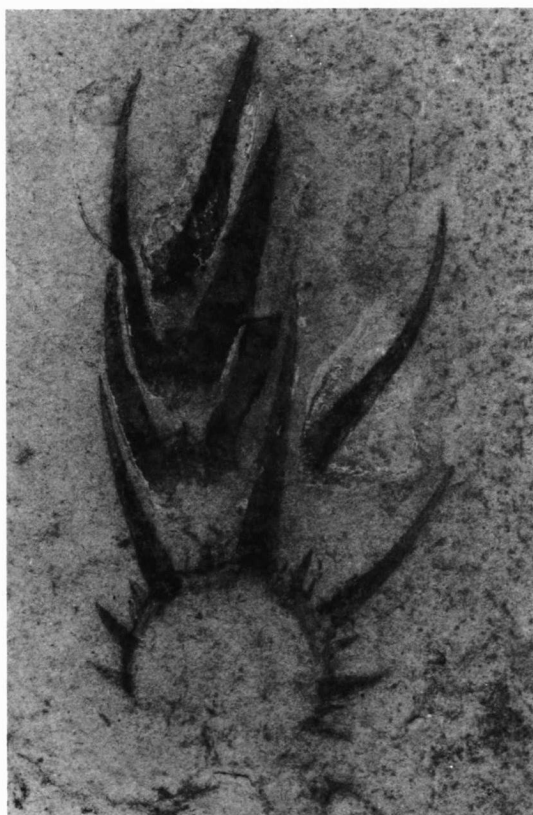
Some specimens (Figs. 5,1,2, 10,1-3) consist of either a disrupted series of whorls or a



1



2a



2b

Fig. 9. *Acinocricus stichus* n. gen. and n. sp. from the Spence Shale, Wellsville Mountains.——1. Detail of distal area of holotype showing subsidiary branches (compare Fig. 5, 3), $\times 5$.——2, a, b. Specimen buried at steep angle to bedding and showing series of spinose whorls; a, part photographed dry; b, counterpart photographed under alcohol; from middle of formation in Miners Hollow; KUMIP 204357, both $\times 3$.

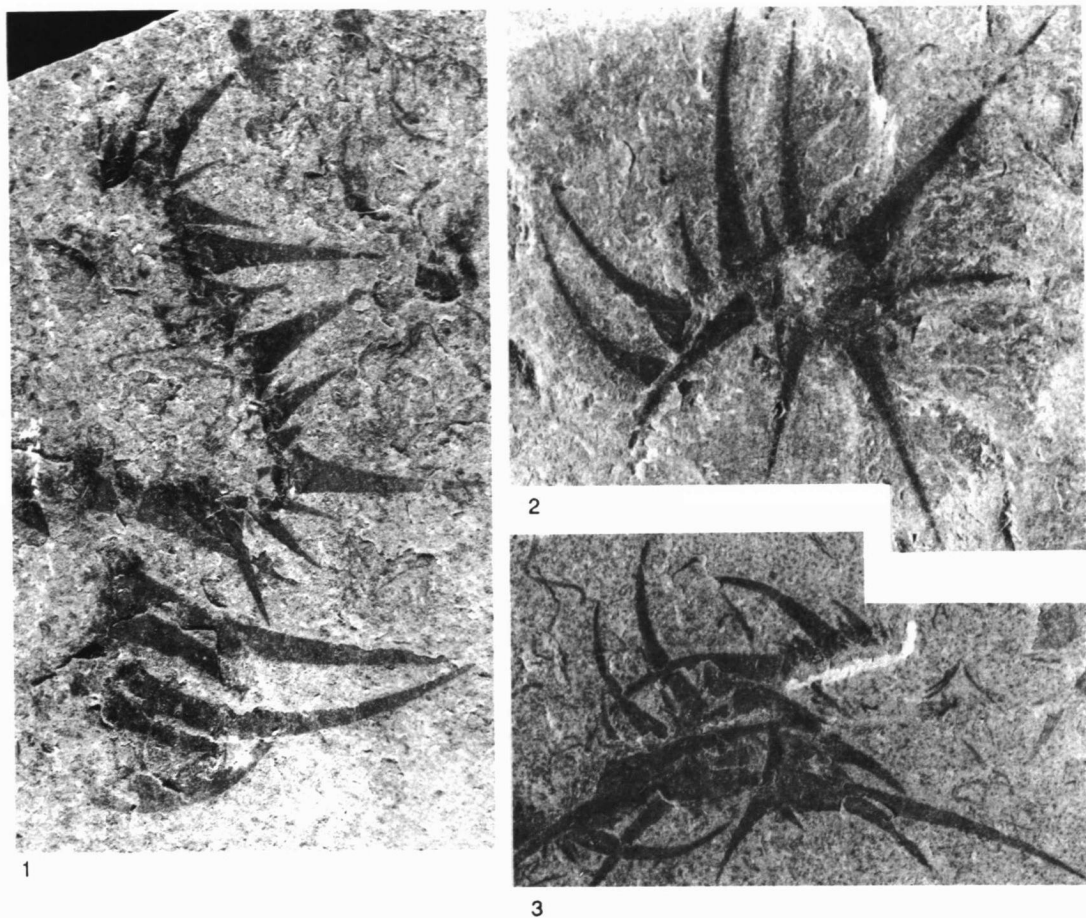


Fig. 10. *Acinocricus stichus* n. gen. and n. sp. from the Spence Shale, Wellsville Mountains.—1. Incomplete series of spinose whorls from Miners Hollow; KUMIP 204358, $\times 3$.—2. Spinose whorl from Miners Hollow; KUMIP 204359, $\times 2.7$.—3. Spinose whorl disrupted by decay, from Donation Canyon; KUMIP 204360, $\times 3$.

single whorl. Such specimens evidently represent the products of increasingly extensive decay but reveal aspects of this alga that are not clearly visible in the more complete specimens. Isolated whorls are typically incomplete, but this may be a reflection of rotting and the processes of detachment from the thallus rather than an original feature. This may be supported by the observation that in rare complete whorls the spines on one side appear to be somewhat shorter, and this region of the whorl may have been somewhat weaker and more prone to decay. Nevertheless, the more common preservation of whorls indicates they were made of

tougher material than that in the remainder of the axis.

In the incomplete specimens, each whorl contains massive spines, ranging up to 15 mm in length, interspersed with much shorter spines that may fall into two size ranges. All the spines, however, are similar in having triangular outlines and a broad base. There is also an indication that the arrangement of spines around a whorl was bilaterally symmetrical, in that counterparts of each spine can be identified on either side of a putative midline (Figs. 5, 2, 9, 2a, b). In one specimen, in which the whorls are disrupted (Fig. 10, 1), shorter spines are

also visible away from the whorl itself. It seems possible that such spines mantled the axis in a zone immediately adjacent to each whorl.

The holotype is unique in bearing additional, small branches at one end of the axis (Figs. 6, 9, 1). These tapering structures cannot be traced directly to the axis, and it is not entirely clear whether they arose from the spinose whorls or from the intervening segments of the axis. Each of these subsidiary branches bears numerous closely spaced spines that project abapically at a moderate angle and may have arisen in whorls.

Discussion.—The repetitive nature of the nodal spinose whorls, possibly also present in the subsidiary branches, strongly suggests this is some type of alga. Its relative complexity and large size argue against its being a member of the Cyanobacteria. The absence of known Cambrian vascular plants and its marine setting, however, suggest that its proper place is within the megascopic prototistans and that similarities to the Equisetales (horsetails) are surely superficial.

Because comparisons between *A. stichus* and other algae are based on gross morphology, without the benefit of data on reproductive organs or cellular structure, conclusions are inevitably tentative. For example, vague similarities could be drawn with the green alga *Draparnaldiopsis* and the red alga *Batrachospermum*, but these forms are substantially smaller. A more intriguing speculation is a possible relationship to the Charales. These are a highly distinctive group of green algae, characterized by the possession of an axis divided into nodes and internodes. The latter give rise to whorls of bracts and sometimes underlying shorter extensions known as stipulodes. The characteristic sex organs (oogonia and antheridia), however, have not been identified in *A. stichus*, and whether the cellular arrangement was comparable is uncertain. In conclusion, therefore, although similarities between *A. stichus* and the Charales could well be superficial, the degree of organization of this Cambrian alga is indicative of an advanced grade. It is in this context that further finds of such algae may be of relevance to documenting forms that might be implicated in the origin of terrestrial floras later in the Paleozoic.

It is not surprising that the fossil record of

noncalcareous algae is very limited and that many supposed species in the older literature require reassessment. So far as we can determine there are no other Cambrian algae (Walcott, 1919; Satterthwait, 1976) that resemble *A. stichus*. Other reports of algae (e.g., Fry and Banks, 1955; Parker and Dawson, 1965; Fry, 1983, and references to older literature therein, nearly all of which we have consulted) do not suggest any useful comparison. The only possible exception is the description of the alga *Chaetocladus* from the Silurian of Wisconsin (Whitfield, 1894; Ruedemann, 1909). This alga has a jointed axis that gives rise to whorls of hairlike filaments. The similarities may well be superficial, and *Chaetocladus* is conspicuously smaller.

Occurrence.—*A. stichus* is known from the upper half of the Spence Shale at a few unnumbered localities in Donation Canyon, Miners Hollow, and Antimony Canyon of the Wellsville Mountains, Utah. The specimens are associated with a lower Middle Cambrian fauna of the *Peronopsis bonnerensis* Zone.

Genus YUKNESSIA Walcott, 1919

YUKNESSIA SIMPLEX Walcott, 1919

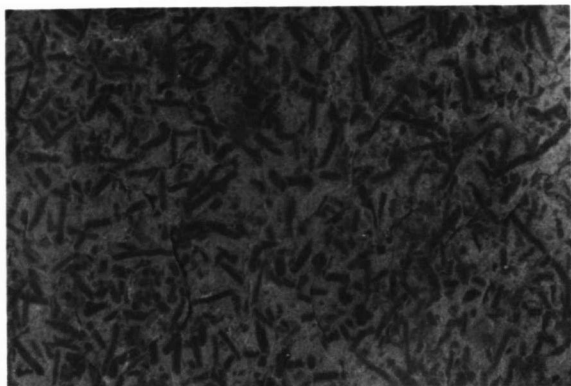
Figure 11

Yuknessia simplex WALCOTT, 1919, p. 235–236, pl. 54, figs. 1, 1a–c; JOHNSON, 1966, p. 38–39, pl. 17, figs. 1–3, 5; GUNTHER and GUNTHER, 1981, pl. 67A.

New material.—More than 20 thalli and numerous stipe fragments. Some specimens were collected by Roger Cooper, Lloyd Gunther, Val Gunther, and Robert Harris.

Emended diagnosis.—Thallus of few to many flexuous stipes; height commonly between 1 and 2 cm, ranging to about 4 cm. Stipes long, slender, and without evidence of jointing or branching; width expanding gradually to about 0.5 to 0.7 mm, rarely to about 1.0 mm. Basal structure comprising tiny, strophically arranged, conical plates, each giving rise to a stipe.

Remarks.—*Yuknessia simplex* was originally described from the Burgess shale quarry and nearby localities in British Columbia (Walcott, 1919). A few new specimens from Utah, supplied by RAR, were described in an un-



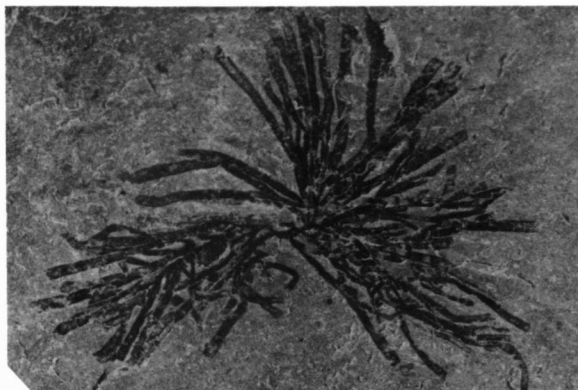
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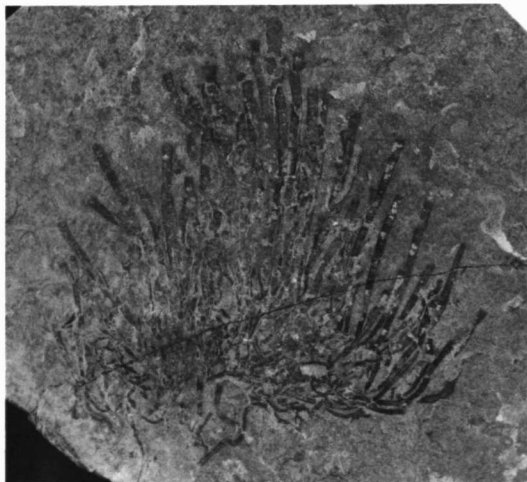
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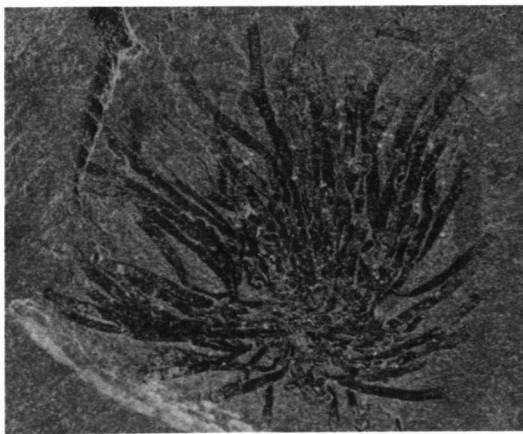
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6

Fig. 11. *Yuknessia simplex* Walcott. —1. Fragments of stipes on multiple parting surfaces of clay shale, middle Marjum Formation, locality 811, House Range; KUMIP 204378, $\times 2$. —2. Small, partly disrupted thalli, upper Wheeler Formation, locality 115, House Range; KUMIP 147909, $\times 2$. —3, 4. Thalli, upper Wheeler Formation, locality 719, Drum Mountains; KUMIP 204379 and 204380, $\times 3$ and $\times 2$, respectively. —5. Large thallus, upper Spence Shale, locality 781, Wellsville Mountains; KUMIP 204381, $\times 1.5$. —6. Thallus, upper Wheeler Formation, locality 115; KUMIP 204382, $\times 2$.

published dissertation by Satterthwait (1976). These and additional specimens from Utah are documented here. Some of the thalli from Utah are greater in height than those described from British Columbia, but differentiation at the species level does not seem to be warranted.

The macroscopic form of *Y. simplex* most closely resembles that of some modern tubular green algae. Such characters as pigment composition, structure of cell walls, and reproductive pattern are heavily weighted in the taxonomy of modern algae (e.g., Round, 1984; Bold and Wynne, 1985). Since these characters are indeterminate in specimens of *Y. simplex*, suprageneric assignment of the species is questionable even at the division level.

Occurrence.—*Y. simplex* is known from British Columbia and Utah. It is present in the following collections from Utah: 781 from the upper Spence Shale of the Wellsville Mountains; 115, 383, and 719 from the upper Wheeler Formation of the Drum Mountains and House Range; and 811 from the middle Marjum Formation of the House Range. The species has an observed stratigraphic range from the *Peronopsis bonnerensis* to the *Ptychagnostus punctuosus* zones of the Middle Cambrian.

Kingdom ANIMALIA

?Phylum CNIDARIA

Class, order, and family uncertain

CAMBRORHYTIUM new genus

Etymology.—From Latin *rhytium*, a drinking horn, combined with an indication of its Cambrian age.

Type species.—*Orthotheca major* Walcott, 1908, p. 243, 246, pl. 1, fig. 11.

Diagnosis.—Tubicolous metazoan. Tube elongate, gradually expanding from apical point to smooth aperture; wall apparently unmineralized and organic in composition, growth by incremental additions producing more or less regular annuli. Operculum lacking.

Discussion.—Walcott (1911c) placed three species in the genus *Selkirkia*: *S. major* (the type species, now referred to as *S. columbia*, see below), *S. gracilis*, and *S. fragilis*. The taxonomy of these species has been the source of some confusion. In brief, the concept of *Selkirkia* and its type species *S. major* was based on tubes with associated soft parts that unequivocally demon-

strate the morphology of priapulid worms (Conway Morris, 1977a). This soft-bodied material is from the phyllopod bed of the Burgess shale, but the holotype of *S. major* (Walcott, 1908) is from the *Ogygopsis* shale on Mt. Stephen. Not only does it lack soft parts, but it is comparable to material that Walcott (1911c) placed in *S. gracilis*. Furthermore, neither *S. gracilis* nor *S. fragilis* can be included in the Priapulida, and their placement in *Selkirkia* is inappropriate. Accordingly, in the interest of nomenclatural stability, Conway Morris (1978) submitted to the International Commission on Zoological Nomenclature that the genus *Selkirkia* be retained for the priapulid worms, best known from the phyllopod bed, and that they be placed in the new species *S. columbia*. This request eventually was accepted (1985, ICZN Opinion 1337, Bulletin of Zoological Nomenclature 42:249–250).

Here, the new genus *Cambrorhytium* is erected to include material formerly attributed to *S. gracilis* and *S. fragilis*. Moreover, *S. gracilis* Walcott, 1911c, is regarded as a junior synonym of *S. major* Walcott, 1908 (see Conway Morris, 1977a:34, 87). *C. fragilis* is much rarer and more poorly known, but available evidence suggests that it is a distinct species.

CAMBRORHYTIUM MAJOR (Walcott, 1908)

Figures 12–15

Orthotheca major WALCOTT, 1908, p. 243, 246, pl. 1, fig. 11.

Selkirkia gracilis WALCOTT, 1911c, p. 120, 122–123, pl. 19, fig. 9; 1912a, p. 153; 1912b, p. 190; HOWELL and STUBBLEFIELD, 1950, p. 12.

Selkirkia SPRINKLE, 1973, p. 182, text-fig. 44; pl. 42, figs. 1–2; pl. 43, fig. 6.

'*Selkirkia*' *major* (Walcott) CONWAY MORRIS, 1977a, p. 34, pl. 15, fig. 1.

'*Selkirkia*' *gracilis* Walcott CONWAY MORRIS, 1977a, p. 34, 87; 1986, p. 428; BRIGGS and CONWAY MORRIS, 1986, p. 177.

Holotype.—Tube lacking soft parts, USNM 96542 (Walcott 1908, pl. 1, fig. 11; Conway Morris 1977a, pl. 15, fig. 1) from the *Ogygopsis* shale of the Stephen Formation (USNM locality 14s), near Field, British Columbia.

Other material.—Approximately 28 spec-

imens from the phyllopod bed of the Burgess shale are in the U.S. National Museum of Natural History. Of these, only USNM 198636 has soft parts preserved. The remainder include USNM 57627, 198637, 198638, 200283, 200285 (counterpart is 400486), 200368 (counterpart is 200384), 200369, 200371, 200385, 200386 (counterpart is 200483), 200393, 200432 (counterpart is 200507), 200455, 200485, 200490, 200512 (counterpart is 200513). Ten specimens were collected from the same bed by members of the Geological Survey of Canada in 1966 and 1967, including GSC 78454 to 78461. GSC 78461 is preserved with soft parts. Additional material is from the *Ogygopsis* shale locality, about 6 km south of the Burgess shale locality (see Fritz, 1971). Two specimens, KUMIP 204361 and 204362, were collected by Val Gunther from locality 716 in the Marjum Formation of the House Range, Utah.

Emended diagnosis.—Tube with variable rate of expansion and transverse annulations, length ranging to 65 mm, original composition organic and probably unmineralized. Soft parts poorly known, consisting of possible tentacular structures extending from aperture of tube.

Description.—With the exception of two or possibly three specimens, this species is known only by its elongate tube (Figs. 12, 13, 15). A size-frequency histogram (Fig. 14) of length for 21 complete tubes from the phyllopod bed reveals a somewhat left-skewed distribution, and the average length is 39.6 mm (total range, 19 to 65 mm). Most of the tubes are complete, but some lack the apical section. If present the apex is finely terminating, and typically the initial part of the tube is somewhat sinuous (Fig. 12, 1-3a, 4). Thereafter, the diameter of the tube increases although the rate of expansion varies rather widely. The aperture of the tube was probably more or less circular and appears to have lacked an operculum. The external surface of the tube is usually annulated (Fig. 12, 3b) although the expression is generally weak. Many specimens show evidence of crumpling or other distortion, which suggests strongly an originally thin wall, probably composed of an organic substance and lacking mineralization.

Soft parts are preserved best in USNM 198636, where about five elongate structures emerge from the apertural region and recurve

to the left side of the specimen (Figs. 12, 3a, b, 13). Their original nature is questionable, and they could perhaps represent tentacles or some supporting structure within the body wall. Fainter strands of tissue appear to connect these elongate structures. Apart from some ill-defined reflective patches within the tube, which might represent soft parts, no other organs are identifiable. In GSC 78461 apparently similar soft parts are visible in the apertural region, but they are poorly preserved and show no significant differences. Within USNM 57627 (Fig. 12, 1a, b), the tube contains an approximately symmetrical structure that tapers rapidly in the anterior but is succeeded by a narrower extension that shows little change in width towards the posterior. Close to the point of constriction are about 6 nodular structures arranged transversely, and these appear to join elongate strands, of which the one on the left side is composed of closely packed nodules. This entire structure is largely preserved as an area of sediment, but conceivably it represents retracted soft parts.

Paleoecology.—*C. major* is assumed to have been a benthic animal. It is always solitary, and there is no evidence that individuals grew together or budded. The tube appears to have lacked anchoring strands or other attachment devices. In one specimen, however, whose placement in *C. major* is not certain because of incomplete preservation, the tube terminates in a rather irregular dark area (Fig. 12, 4) that may represent a foreign body used for attachment. Unless the tube lay on the sediment, it is likely that it was partially embedded. Growth was by marginal additions to the apertural region, resulting in the annulations on the tube wall. If the elongate extensions of soft tissue represent tentacles, then *C. major* may have been either a suspension feeder or carnivore, the latter perhaps being more likely if a cnidarian affinity is supported (see below).

Discussion.—With two exceptions, all available specimens of *C. major* are from the Stephen Formation, British Columbia. The best preserved specimens, including those with soft-part preservation, come from the phyllopod bed. The tubes from the Marjum Formation, Utah (Fig. 15), have a somewhat narrower apical length than do most tubes from British Columbia but are otherwise very similar in



1a



1b



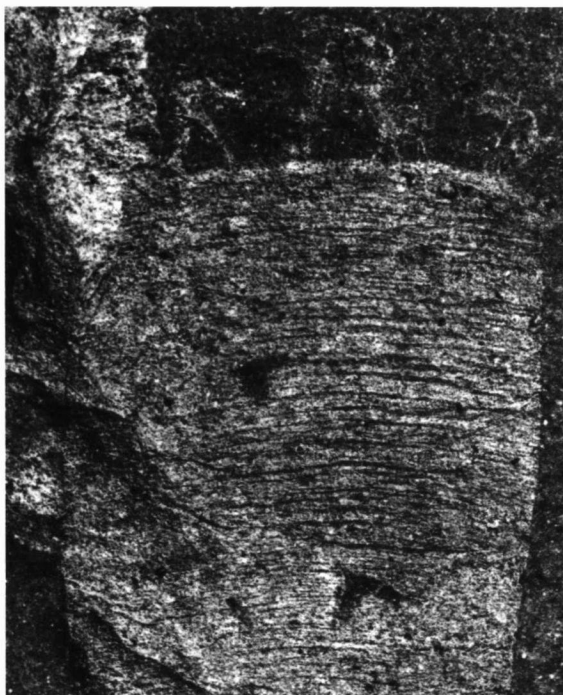
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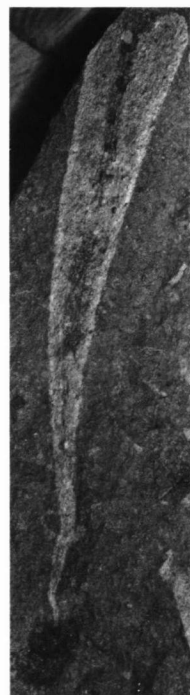
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3a



3b



4

Fig. 12. *Cambrorhytium major* (Walcott) from the phyllopod bed of the Burgess shale (1-3) and the *Ogygopsis* shale (4), Stephen Formation, British Columbia. —1. Holotype, tube with possibly retracted soft parts, USNM 57627; a, photographed under high-angle UV radiation, $\times 2.2$; b, photographed under low-angle UV radiation, $\times 2.2$. —2. Tube, USNM 198637, photographed under high-angle UV radiation; a, $\times 2.2$; b, detail of proximal end, $\times 6.7$. —3. Tube with soft parts, USNM 198636; a, photographed under high-angle UV radiation, $\times 2.2$; b, detail of soft parts (compare Fig. 13), photographed under alcohol, $\times 7.2$. —4. Incomplete tube with possible attachment structure, photographed under high-angle UV radiation; USNM 198638, $\times 3$.

overall shape and dimensions. In passing, it is worth noting that a similarity, possibly superficial, may exist with tubes from the Lower Cambrian (Tommotian Stage) of Siberia that are referred to *Torelloides giganteum* (see Sokolov and Zhuravleva, 1983:159, pl. 60, fig. 3).

Despite Walcott's (1911c) inclusion of *C. major* (as *S. gracilis*) with the priapulid *S. columbia*, no such systematic association can be demonstrated. The tubes differ, with that of *C. major* tapering to a fine termination, whereas in *S. columbia* the tube is more parallel-sided and has an open posterior end. The soft parts of *C. major* are difficult to reconcile with the priapulid proboscis that protrudes from the tube of *S. columbia*, even if allowance is made for extensive decay.

Despite poor preservation of the soft parts, comparisons may be drawn with the cnidarians. The elongate structures that extend from the aperture of the tube resemble the oral tentacles that characterize both the hydroid and medusoid stages. Assuming that the animal possessed a gut, then the closed apex of the tube suggests

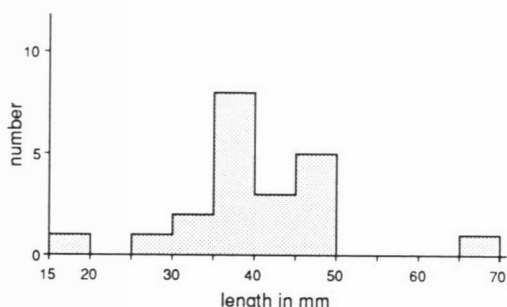


Fig. 14. Size-frequency histogram of length, in mm, for 21 tubes of *Cambrorhytium major* (Walcott) from the phyllopod bed of the Burgess shale; mean is 39.6 mm, standard deviation is 9.33.

that either the alimentary canal was recurved or (as in cnidarians) the mouth and anus shared the same opening.

Some support for a cnidarian affinity may come if a relationship can be demonstrated between *C. major* and the genus *Byronia*. This tubicolous fossil was first described as *B. annulata* by Matthew (1899, pl. 1, fig. 2; see also Walcott, 1908, pl. 1, figs. 9, 9a) from the *Ogygopsis* shale of the Stephen Formation. Worm tubes from the Kaotai and Aoxi formations (lower Middle Cambrian) of western Hunan, China, were placed in the new genus *Scolecicellus* by Liu (1986), but they may possibly be attributed to *Byronia*. Liu (1986) interpreted the tube annulations as body somites and evidently misidentified the internal surface at one end of the tube as a head. Strikingly similar tubes have also been described from the Tommotian Stage of Siberia as *Hyolithellus grandis* (Missarzhevsky, 1969:151–152, pl. 2, fig. 2). In addition to these occurrences, Ordovician material from erratic boulders of Poland has also been attributed to *Byronia* (Kozłowski, 1967, figs. 2, 3, 6; Mierzejewski, 1986, figs. 4, 5, pl. 19, figs. 1–7). Differences between the Polish species (*B. naumovi*, *B. robusta*) and the type species *B. annulata*, which include tube size and ornamentation, were commented on by Kozłowski (1967) and Mierzejewski (1986). Whether those differences extend also to the ultrastructure of the tube wall as documented by Mierzejewski (1986) in the Polish material remains to be determined.

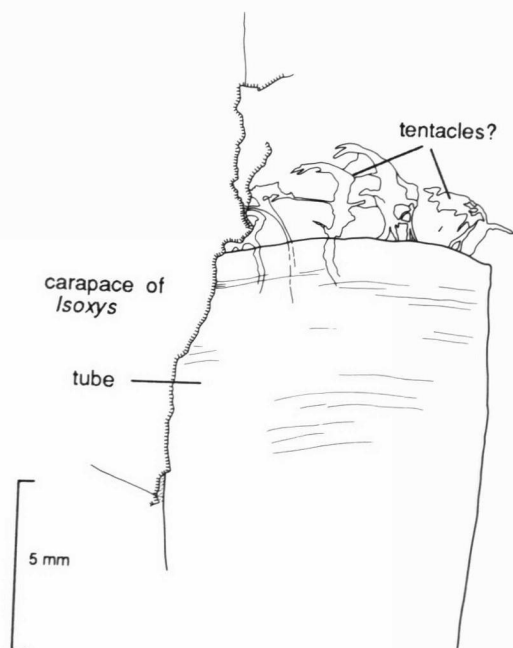


Fig. 13. *Cambrorhytium major* (Walcott), USNM 198636, explanatory drawing of anterior region to show soft parts (compare Fig. 12,3b).

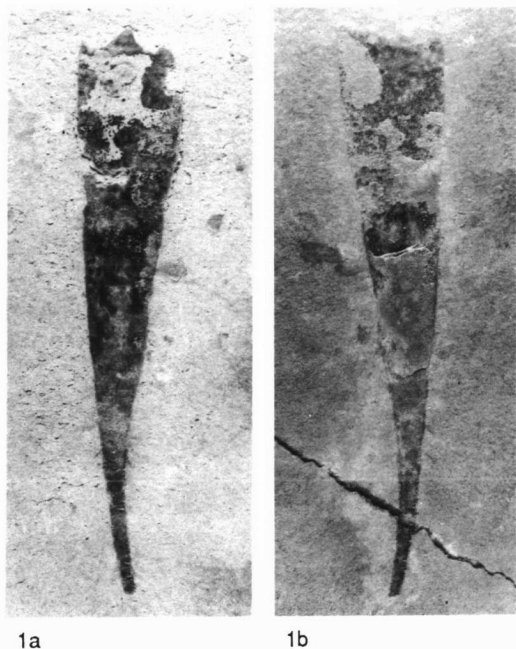


Fig. 15. *Cambrorhytium major* (Walcott), part (1a) and counterpart (1b) of tube from locality 716, Marjum Formation, House Range; KUMIP 204361, both $\times 1.5$.

Howell (1962) followed Matthew (1899) in suggesting an annelid affinity for *Byronia*. More convincing, however, is Kozłowski's (1967) comparison of *Byronia* with the sedentary stage (or polyp generation) in the coronate scyphozoan life cycle where the scyphopolyps inhabit an organic (questionably chitinous) tube that is referred to as a scyphothecae. Well-known genera with this type of development include *Stephanoscyphus* and *Nausithoe* (see Werner, 1979; cf. Mierzejewski, 1986:144). Notwithstanding Werner repeatedly (e.g., 1967, 1973, 1979) drawing attention to similarities between the scyphothecae and the extinct Conulata (but see Babcock and Feldmann, 1986; Feldmann and Babcock, 1986), the descriptions of recent scyphothecae appear rather to reinforce Kozłowski's (1967) comparison, especially with respect to *B. annulata*. As noted above, ultrastructural investigations of *B. annulata* could help to confirm or refute this comparison. Given broad similarities in tube morphology and more tentative indications from the soft tissues, it seems possible that *C. major* should also be included in such comparisons.

Occurrence.—*C. major* is known from the Stephen Formation (*Ogygopsis* shale and Burgess shale localities) of British Columbia and the upper Marjum Formation of Utah. It ranges from the lower Middle Cambrian (*Glossopleura* Zone) to the upper Middle Cambrian (*Ptychagnostus punctuosus* Zone).

CAMBORHYTIUM FRAGILIS (Walcott, 1911c)

Figure 16

Selkirkia fragilis WALCOTT, 1911c, p. 120, 122, pl. 19, fig. 8; 1912b, p. 190; HOWELL and STUBBLEFIELD, 1950, p. 12; CONWAY MORRIS, 1977a, p. 34, 87.
'*Selkirkia*' *fragilis* (Walcott) BRIGGS and CONWAY MORRIS, 1986, p. 177.

Holotype.—Tube, USNM 57626 (Walcott 1911c, pl. 19, fig. 8, and herein Fig. 16, 1a, b), from the *Ogygopsis* shale of the Stephen Formation (USNM locality 14s) near Field, British Columbia.

Other material.—Three specimens, one from the *Ogygopsis* shale (USNM 198640) and two from the phyllopod bed of the Burgess shale (USNM 198639, 276182).

Diagnosis.—Tube with relatively low length to width ratio, transverse annulations usually obscure, originally organic composition. Soft parts not known.

Description.—In this rare species the wall of the tube characteristically is preserved as a highly reflective material (Fig. 16, 1-3). The tubes range in length from about 9 to 25 mm. Two tubes taper to fine terminations (Fig. 16, 1, 2). In a third the apex is truncated and a series of strands project for a distance of about 1.5 mm (Fig. 16, 3), and in a fourth (USNM 276182) the apex is broken. The tube wall appears to be more or less structureless, except for closely spaced annulations (about 15 per mm) near the apex. The tubes are otherwise relatively featureless and lack an operculum or preserved soft parts.

Paleoecology.—The mode of life is inferred to have been similar to that of *C. gracilis*. The proximal strands in one specimen may have acted as anchors, but their development may have been a response to damage to the apex.

Discussion.—*C. fragilis* differs from *C. major* in the proportions of the tube, having a gen-

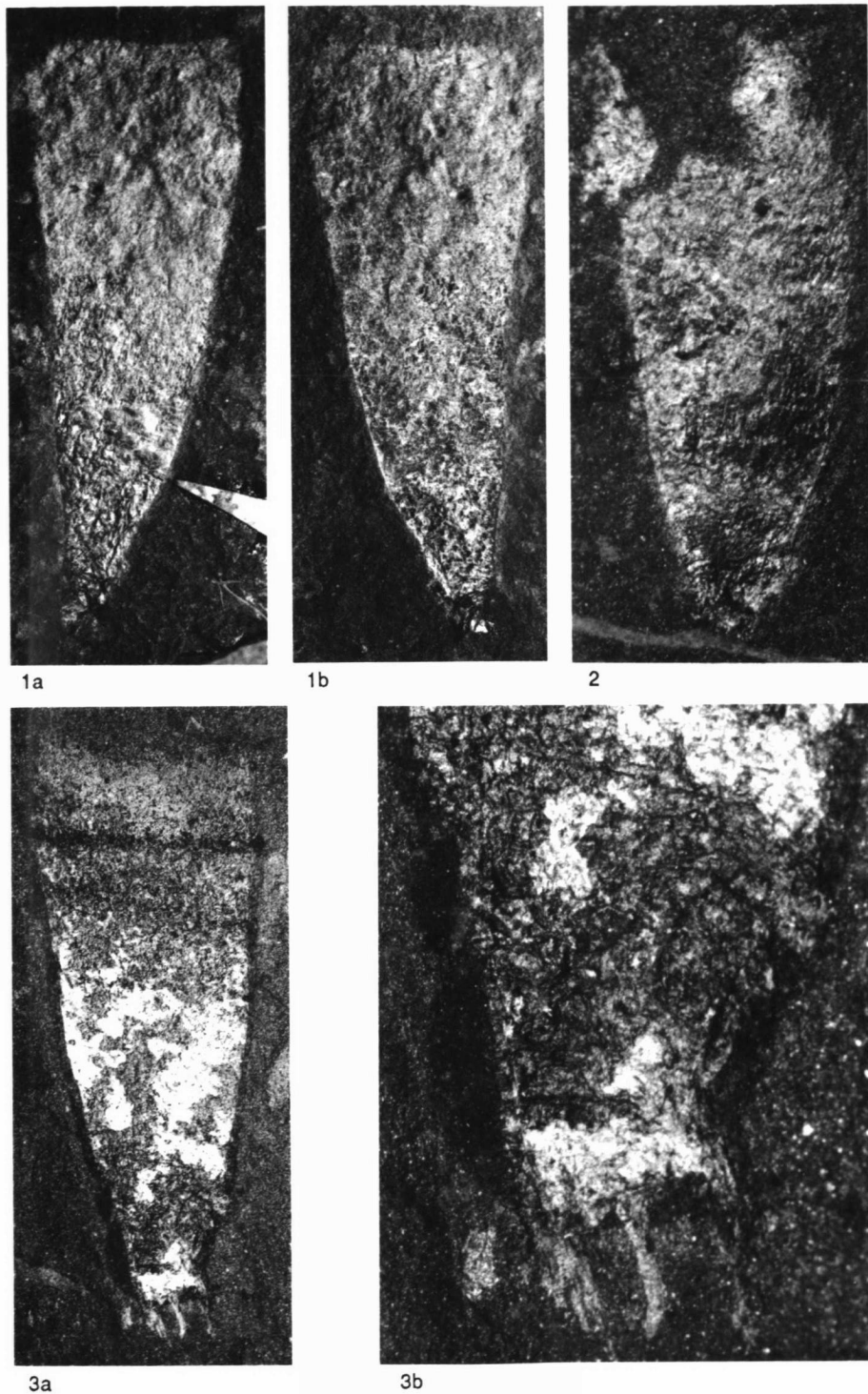


Fig. 16. *Cambrorhytium fragilis* (Walcott) from the Stephen Formation, British Columbia; all photographed under high-angle UV radiation.—1. Holotype tube from *Ogyopsis* shale locality, part (a) and counterpart (b); USNM 57626, both $\times 3$. —2. Tube from *Ogyopsis* shale locality; USNM 198640, $\times 8.9$. —3. Tube from phyllopod bed of Burgess shale locality, USNM 198639; a, $\times 4.9$; b, detail of proximal end, $\times 14$.

erally lower length to width ratio. The strikingly reflective nature of the wall may point also to a somewhat different original composition.

Occurrence.—Stephen Formation (*Ogygopsis* shale and Burgess shale localities), British Columbia.

Phylum PRIAPULIDA

Class and order uncertain

Family SELKIRKIIDAE Conway Morris,
1977a

Genus **SELKIRKIA** Walcott, 1911c

The tubicolous genus *Selkirkia* was originally described from the phyllopod bed of the Burgess shale, but this priapulid is now known to have wide distribution in the upper Lower Cambrian (Pennsylvania: Kinzers Formation) and most of the Middle Cambrian (Utah, Idaho, and British Columbia: Marjum, Wheeler, Spence, and Stephen formations). The genus is represented by *S. columbia* Conway Morris, 1977a (type species), *S. pennsylvanica* Resser and Howell, 1938, *S. spencei* Resser, 1939, and *S. willoughbyi* Conway Morris and Robison, 1986.

SELKIRKIA sp. cf. **S. COLUMBIA**
Conway Morris, 1977a

Figure 17

New material.—Three tubes were collected by Val Gunther from the middle part of the Spence Shale in Antimony Canyon of the Wellsville Mountains, Utah. All are compressed in dark-gray, noncalcareous, mudshale. Two tubes (KUMIP 204363, 204364; Fig. 17) are on the same slab in association with algal debris. On one of the tubes (204363) is a series of narrow burrows that are presumed to have been impressed by sediment compaction. The third tube (KUMIP 204365) is associated with remains of the alga *Acinocriscus stichus* n. gen. and n. sp.

Description.—All three tubes lack soft parts. The associated tubes are each about 32 mm long and have similar ratios of posterior to anterior widths (about 1.0:1.8), and so accord with broad-aspect specimens as defined by Conway Morris (1977a:37; text-fig. 20). KUMIP 204365 is about 44 mm long, and despite being incomplete appears to be somewhat more tapered.

Discussion.—Hitherto, all specimens of *Selkirkia* from the Spence Shale have been assigned

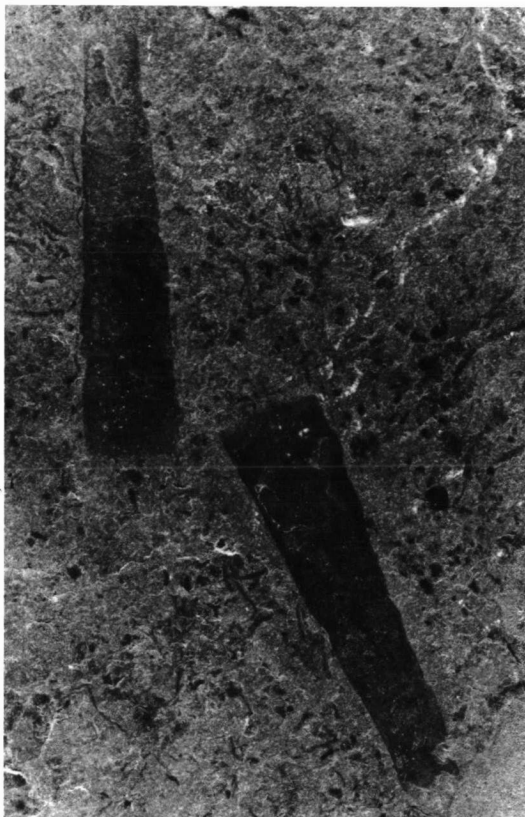


Fig. 17. Tubes of *Selkirkia* sp. cf. *S. columbia* Conway Morris from the Spence Shale, Utah; KUMIP 204363 (left) and 204364 (right), $\times 1.7$.

to *S. spencei*, which is characterized by the sides of the tube being near parallel (Resser, 1939) and a relatively large adult size (tubes exceeding 70 mm; Conway Morris and Robison, 1986). In *S. columbia* variations in the rate of apertural expansion in specimens from the Burgess shale were used to argue that originally the tube had an oval cross section, with the appearance of a given specimen depending on the angle of burial (see Conway Morris, 1977a). In *S. spencei* the parallel edges of the tube in all specimens suggests that the transverse cross section may have been more circular. The maximum size reached by *S. spencei* in comparison with the somewhat smaller *S. columbia* has also been regarded as significant. The specimens described here, however, seem to be more similar to those of *S. columbia*. Although *S. columbia* and *S. spencei* may be synonyms, their

specific identity is at present maintained. These new specimens, therefore, suggest a significant increase in the stratigraphic and geographic ranges of *S. columbia*.

Phylum ARTHROPODA

Class TRILOBITA

Order NEKTASPIDA

Family NARAOIIDAE Walcott, 1912a

Genus NARAOIA Walcott, 1912a

A brief description of abundant specimens of *Naraoia* with soft parts and appendages in the Chiungchussu Formation of eastern Yunnan, China (Zhang and Hou, 1985), has substantially extended the observed geographic and stratigraphic distributions of the genus. Associated trilobite species are some of the oldest known in China and perhaps the world, being thought to correlate temporally with early At-dabanian faunas of the Soviet Union (Zhang Wen-tang, personal communication, 1986). *Naraoia* has an observed range throughout most of the Lower and Middle Cambrian (*Eoredlichia-Wutingaspis* to *Ptychagnostus punctuosus* zones) and the greatest observed stratigraphic range of any Cambrian trilobite genus. Its distribution in both North America and Asia suggests that it may be discovered on other continents as well.

NARAOIA COMPACTA Walcott, 1912a

Figure 18

Naraoia compacta WALCOTT, 1912a, p. 175–177, pl. 28, figs. 3, 4; ROBISON, 1984b, p. 2–7, figs. 1–3 (for synonymy to date).

New material.—Two specimens, both strongly compressed dorsoventrally, are preserved in light-gray, argillaceous, lime mudstone. The best preserved specimen (USNM 424112, Fig. 18), collected by P. E. Reese, is complete and represented by part and counterpart. At the time of burial, it appears to have been oriented with the cephalon inclined anteriorly and the pygidium inclined posteriorly (terminology *sensu* Robison, 1984b:2). With vertical compaction, the length of each tagma was shortened relative to its width. The body has separated along a horizontal plane, exposing a large dark area in the position of the midgut and lateral diverticula within the head. Portions of the hindgut and vestiges of several segments are

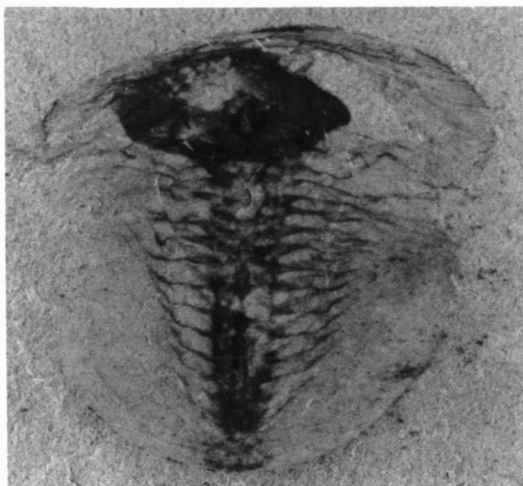


Fig. 18. Counterpart of *Naraoia compacta* Walcott from upper Wheeler Formation, locality 116, House Range, Utah; USNM 424112, $\times 3$.

indicated by dark markings along the middle of the trunk.

The second specimen (USNM 424113), collected by Lloyd Gunther, is a poorly preserved pygidium. It is 19 mm long and 15 mm wide, which is within the limits of variation recorded for specimens of *N. compacta* from the Burgess shale (Whittington, 1977, fig. 2,d).

Discussion.—*N. compacta* has previously been described from Utah (Robison, 1984b), but these are the first specimens to be reported from the Wheeler Formation. Although adding no morphological information, they do support the suggestion that *Naraoia* was a common member of the Cambrian biota of China and North America. An apparent lack of calcite in the exoskeleton probably accounts for the rare preservation of specimens.

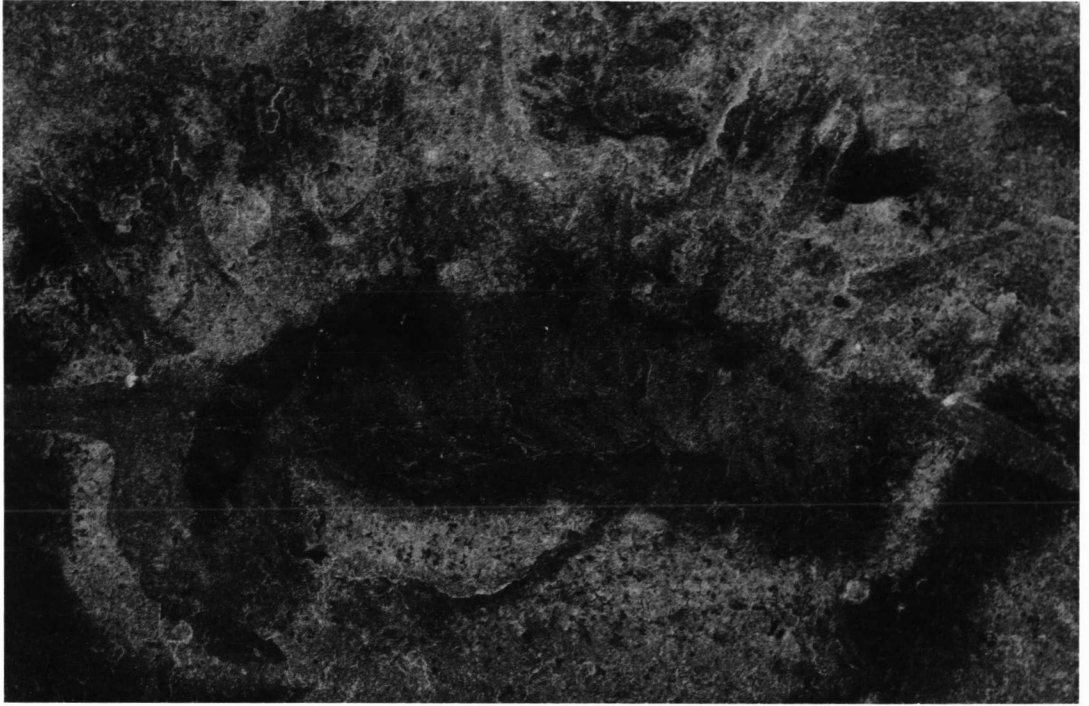
Occurrence.—The new specimens are from locality 116 in the upper Wheeler Formation of the House Range, and they are associated with a fauna characteristic of the upper half of the *Ptychagnostus atavus* Interval-zone (Robison, 1984a).

Class and Order uncertain

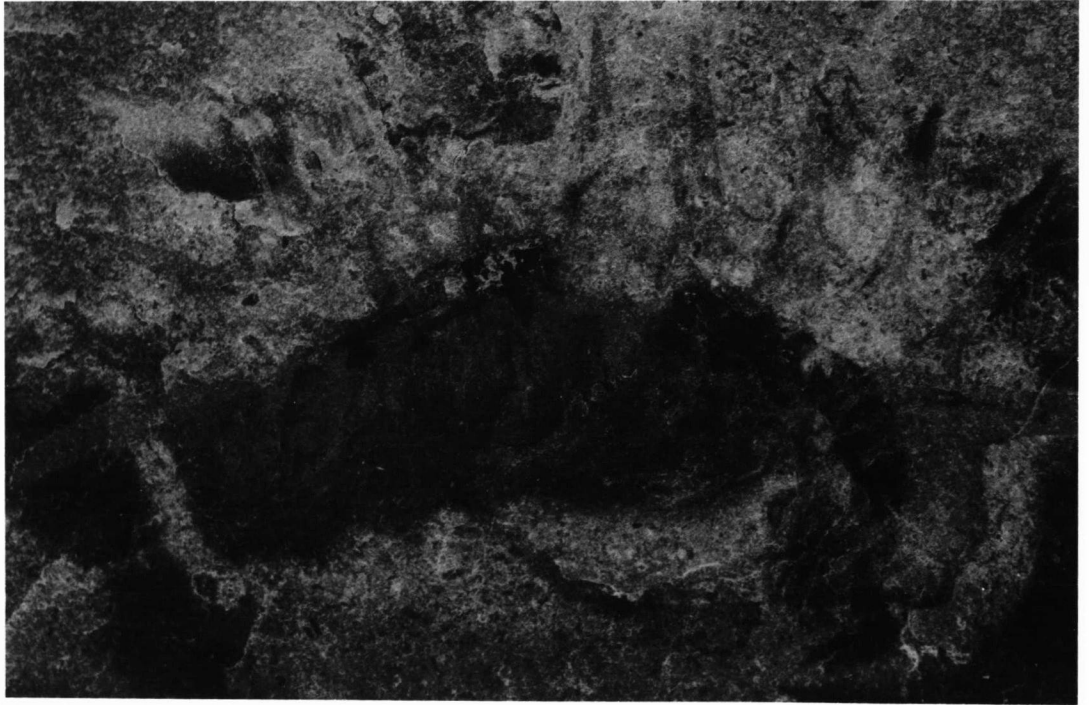
?Family MOLLISONIIDAE Simonetta and Delle Cave 1975

ECNOMOCARIS new genus

Etymology.—Greek *eknomos*, wonderful and



1a



1b

Fig. 19. *Ecnomocaris spinosa* n. gen. and n. sp. Body of holotype from upper Wheeler Formation, locality 115, House Range; part (1a) and counterpart (1b); USNM 424114, both $\times 2$.

monstrous, in reference to the remarkable appearance of this animal.

Type species.—*Ecnomocaris spinosa* n. sp. (Figs. 19, 20).

Description.—Body elongate; consisting of 11 or more probable somites, each bearing a mediodorsal, elongate spine. Spine on inferred anterior end extending forward; length greater than that of body. Head and tail regions poorly defined, but intervening questionable tergites apparently bear pleurae. Possible appendages very poorly defined.

Discussion.—This new genus is represented by a single specimen, showing only moderate preservation. Many aspects of its anatomy remain uncertain, and even unequivocal distinction between the anterior and posterior is not possible. Despite its bizarre appearance similarities to the Burgess shale arthropods *Thelxiope* Simonetta and Delle Cave, 1975, and more distantly *Habelia* Walcott, 1912a, may be significant.

ECNOMOCARIS SPINOSA new species

Figures 19, 20

Etymology.—From Latin *spinus*, thorny; in reference to the prominent spines.

Holotype.—Represented by part and counterpart, USNM 424114. It was collected by Edward Cole at a commercial quarry in the upper Wheeler Formation at its type locality in Wheeler Amphitheater, House Range, Utah. The specimen is laterally compressed in medium dark-gray, argillaceous, lime mudstone.

Description.—The only known specimen (Figs. 19, 20) consists of an elongate body. It is recurved at either end, giving the specimen an arcuate shape. If straightened, the body length without anterior and posterior spines would be approximately 7 cm, but with spines the length would probably exceed 18 cm. Functional considerations (see below) suggest that the series of elongate spines was dorsal, so that the concave side of the specimen presumably represents the ventral region. The body appears to have been covered by an exoskeleton that was probably unmineralized. Somite divisions, in particular zones of articulation between the tergites, are not visible, although this may be the consequence of the relatively poor preservation. Towards the ventral side features of the exoskeleton become more obscure, but recurved

structures may represent pleural lobes, possibly composed of unusually thin cuticle. If these pleurae are correctly identified, their direction of curvature is presumably towards the posterior. Details of both the anterior and posterior ends are obscure, but so far as can be discerned they were relatively simple and may have formed smooth cephalic and posterior shields.

On the dorsal side is a prominent series of spines (Fig. 20) that appear to form a single file along the midline. They total 11, with those at either end being conspicuously longer than the intervening 9 spines. At the presumed anterior end the spine extends for at least 83 mm, with its distal termination unknown due to rock breakage. Its proximal length is more or less straight, but thereafter it is gently arcuate and bends ventrally. The posteriormost spine is incompletely exposed, but judging by its rate of tapering it was considerably shorter and may not have exceeded about 30 mm. The intervening spines are relatively stout and have an average length of about 12 mm, although the anteriormost of the 9 spines appears to have been slightly longer. Because the somite divisions are so obscure, it cannot be determined whether the 11 spines correspond to trunk divisions alone or include also the cephalic and posterior regions. As noted below, however, possible equivalents to spine numbers in *Thelxiope* from the Burgess shale may be a significant guide.

Apart from the exoskeleton, little is known of this animal. The ventral region bears very obscure structures that conceivably represent appendages (Figs. 19, 20), but no details are discernible. A prominent longitudinal strand that can be traced along much of the body is interpreted as the alimentary canal. Areas of negative relief presumably represent infill, but its exact nature is uncertain. Diffuse and generally dark areas that surround much of the ventral region are taken to represent traces of organic material that oozed from the carcass after death.

Paleoecology.—It seems likely that *E. spinosa* was benthic and presumably had walking legs. The primary function of the spines is assumed to have been defensive, protecting the animal from predators. In particular, the elongate anterior and posterior spines may have provided advanced warning of possible attack, while the

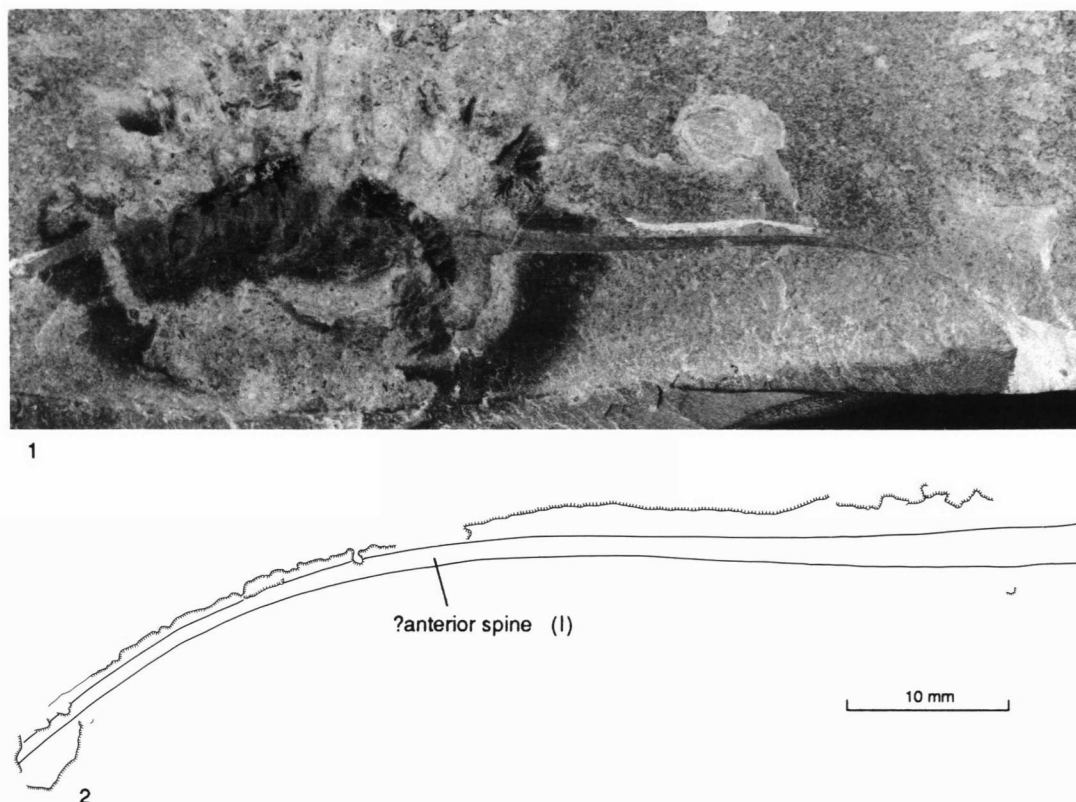


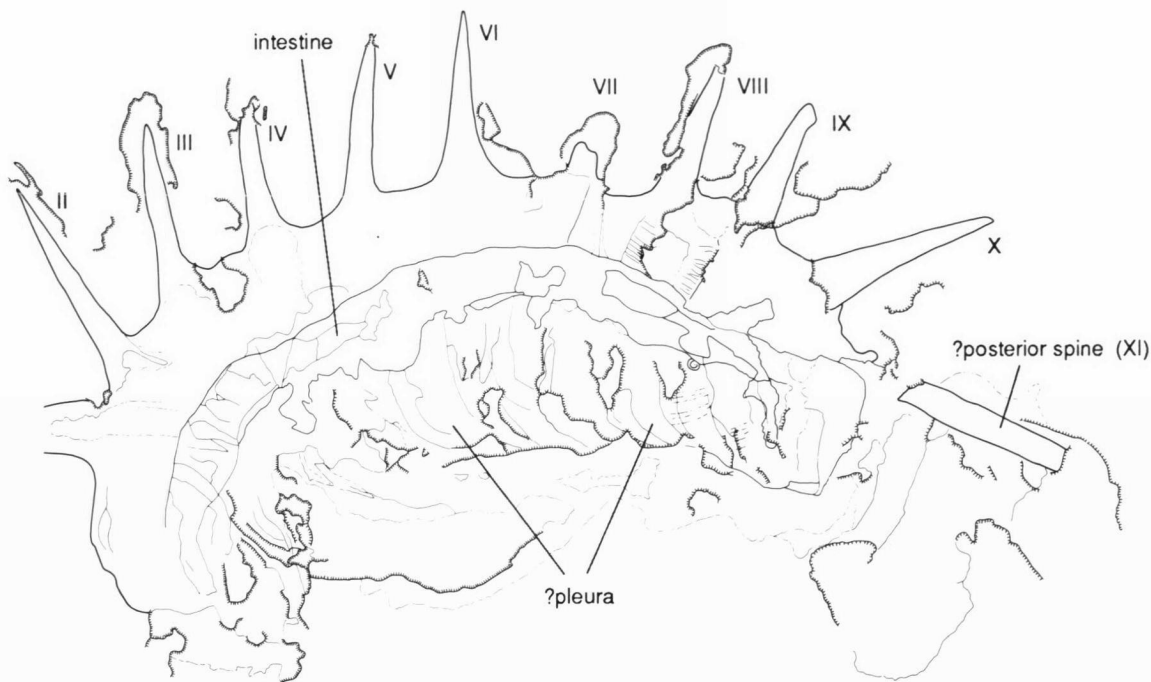
Fig. 20. *Ecnomocaris spinosa* n. gen. and n. sp., USNM 424114. —1. Holotype counterpart, $\times 0.9$. —2. Explanatory drawing of holotype with details of the counterpart transferred by reversal (compare Fig. 19).

stout intervening spines may have provided physical protection. The contents of the gut appear to be fine grained. If original rather than a diagenetic infilling (see Briggs and Whittington, 1985:152), they suggest that the animal may have been a deposit feeder (collector), but the details of food manipulation are not known.

Affinities.—The elongate spines arising from one side of the body recall the enigmatic metazoan *Hallucigenia sparsa* Conway Morris, 1977b, but detailed comparisons show that the resemblances are superficial. Although details of the exoskeleton and its putative appendages are obscure, *E. spinosa* seems best interpreted as an arthropod. In particular, similarities are evident with the rare Burgess shale arthropod presently known as *Thelxiope palaeothalassia* Simonetta and Delle Cave (1975, pl. 3, fig. 1; pl.

22, figs. 3–5; see also Simonetta, 1964, text-fig. 3, pl. 38). The three specimens known to Simonetta were originally included as paratypes of *Parahabelia rara* (Walcott, 1912a); *Parahabelia* is a genus erected by Simonetta (1964) to include material originally referred to *Mollisonia*? *rara* (Walcott, 1912a, pl. 24, figs. 6, 7; Walcott, 1931, pl. 21, fig. 4). Subsequently, however, Simonetta and Delle Cave (1975:5) decided that its attribution to *Mollisonia* (misspelled by them *Mollinsonia*) was correct and that *M. rara* might even be a synonym of the type species, *M. symmetrica* Walcott, 1912a. Note also that Simonetta and Delle Cave (1975:32) misspelled their newly erected family as Mollinsoniidae rather than Mollisoniidae.

Arthropods presently included in *T. palaeothalassia* are more or less isopygous, with each of the seven thoracic segments bearing a promi-



nent dorsal spine. Simonetta (1964, text-fig. 3) depicted only six such segments. In addition, the posterior shield is composed of three segments of which the last one bears an elongate spine that slightly exceeds the length of the rest of the body (spine to body-length ratio in USNM 144914 is 1.0:1.2). There is also some evidence that the remaining two segments bear spinose projections. An undescribed specimen in Geological Survey of Canada collection 78462 has what appears to be a broad dorsal spine on the first segment of the tail shield, whereas the second segment may have a much more subdued spine. Possibly similar structures are present in USNM 144916, but they are not clearly visible in Simonetta's illustration (1964, pl. 38, top figure). In another specimen (USNM 144915), the posterior part of the dorsal cephalon bears a short spine. Thus, if all of these dorsal projections are accepted as

original, *T. palaeothalassia* had a complement of 11 spines (see below).

As Simonetta (1964) noted, these specimens of *T. palaeothalassia* are very similar to those of *M. rara*, and he even speculated that they could represent sexual dimorphs. The only obvious difference is the absence of spines in *M. rara*. Such features of *M. rara* as a broad notch on the ventral cephalic margin and the form of its thoracic pleurae are strikingly similar to those of *T. palaeothalassia*. It seems unlikely, however, that the spines could be absent because of either postmortem breakage or inappropriate angles of burial, although in USNM 57663 (Walcott, 1912a, pl. 24, fig. 7) breakage along the dorsal and posterior margins makes it difficult to decide whether or not spines were originally present. However, the elongate structure that arises from the anterior of this specimen appears to have resulted from chance superposi-

tion, although the nature of this ostensibly foreign body is not readily recognizable. Moreover, in *Mollisonia gracilis* Walcott, 1912a, which is evidently closely related to *M. rara* and the type species *M. symmetrica*, some specimens show a carinate structure on the midline of each thoracic segment, which may represent a spine.

E. spinosa differs from *T. palaeothalassia* in being substantially larger, although the body of one specimen (the now incomplete USNM 144916) of *T. palaeothalassia* originally was about 25 mm long, giving a total length with the posterior spine of more than 50 mm. Moreover, Walcott (1912a:198) noted that *M. rara* may have reached "a length of from 5 to 6 cm," and later he illustrated (Walcott, 1931, pl. 21, fig. 4) a specimen (USNM 83951) that is about 68 mm long. The exoskeleton of *E. spinosa* has elongate spines on both the anterior and posterior, whereas *T. palaeothalassia* has a prominent spine only on the presumed posterior, and the anterior spine is much shorter. Moreover, if the distinction between anterior and posterior ends in *E. spinosa* is correct, then the relative lengths of its respective spines would seem to be opposite to that of *T. palaeothalassia*. However, accepting the comparisons between these spines, it seems also possible to identify equivalents to the remaining nine dorsal spines. Thus, seven of the spines may be matched to the equivalent number of thoracic spines in *T. palaeothalassia*, while the remaining two would then compare to the short triangular extensions that appear to be identifiable on the first two segments of the fused tail shield (see above).

Simonetta and Delle Cave (1975) also claimed a close relationship between *T. palaeothalassia* and *Habelia optata* Walcott, 1912a. A detailed redescription of *H. optata* by Whittington (1981) showed that the first three thoracic segments have short dorsal spines, although in the context of the discussion above it may also be significant that in some specimens these spines may be greatly reduced or absent. The posterior segment has an elongate spine, but other similarities with *E. spinosa* are rather general. Another species questionably placed in *Habelia* (*H.?* *brevicauda* Simonetta, 1964) by Whittington (1981) is poorly known and seems to be less similar to *E. spinosa*. Finally, it is worth noting a form from locality 9 of Collins, Briggs, and Conway Morris (1983)

in the Stephen Formation on Mt. Stephen, British Columbia. This fossil was referred to by Collins (1986:39) as a "new spiny animal." The one specimen to be illustrated is about 40 mm long and bears possibly six anterior pairs of legs, with a prominent array of spines on the inner surfaces, succeeded by a series of posterior segments. On the dorsal surface a series of spines, totaling five or six in one specimen, are arranged apparently along the midline. While the spines are somewhat similar to those of *Ecnomocaris* and *Thelxiope*, other details of the anatomy appear to differ, although the absence of appendages in these latter taxa hinders comparison.

Family uncertain

UTAHCARIS new genus

Etymology.—A combination of the name Utah and Latin *caris*, shrimp; in reference to the place of origin of the fossil and in allusion to its general arthropodan aspect.

Type species.—*Utahcaris orion* n. sp. (Figs. 21, 22).

Description.—Dorsal exoskeleton long and slender, axis undefined. Cephalic shield subtriangular with rounded posterolateral corners, eyes not evident. Trunk containing 11 tergites and a subcircular, dorsoventrally flattened, laterally spinose telson. Cephalic shield and telson subequal in size. Appendages not known.

Discussion.—The affinities of *Utahcaris* within the Arthropoda remain unclear in the absence of information about appendages. It differs from all Cambrian arthropods in the structure of its large, subcircular telson. It is similar to *Actaeus* Simonetta, 1970, *Alalcomenaeus* Simonetta, 1970, *Leancoilia* Walcott, 1912a, and *Sanctacaris* Briggs and Collins, 1988, in having a rather featureless cephalic shield and 11 trunk tergites. *Actaeus* (Whittington, 1981) and *Leancoilia* (Bruton and Whittington, 1983), however, have a smaller telson that is spinelike, and *Sanctacaris* has a posteriorly expanded telson. The telson of *Alalcomenaeus* is known only in lateral view (Whittington, 1981) but probably differs from that of *Utahcaris*. Also, *Actaeus*, *Alalcomenaeus*, and *Sanctacaris* have marginal eyes, and in *Actaeus* the trunk tergites decrease in sagittal length toward the posterior, whereas *Utahcaris* lacks evidence of eyes and its

trunk tergites increase in length toward the posterior.

Mollisonia Walcott, 1912a, which is poorly known, has a telson comparable in size to that of *Utahcaris*, but it has four less trunk tergites. Also, the telson appears to be quadrate rather than subcircular and is posteriorly rather than laterally spinose.

Utahcaris presently includes only its type species from the Spence Shale of early Middle Cambrian age in the Wellsville Mountains, Utah.

UTAHCARIS ORION new species

Figures 21, 22

Etymology.—Latin *Orion*, fabled hunter; in reference to possible predatory habits of the animal.

Holotype.—Part and counterpart, KUMIP 204784, collected by Benjamin F. Dattilo from the middle part of the Spence Shale in Antimony Canyon, Wellsville Mountains, Utah.

Other material.—Part and counterpart of one specimen, KUMIP 204785, collected by Robert and Nancy Meyers from the upper six meters of the Spence Shale in Miners Hollow, Wellsville Mountains, Utah.

Description.—The holotype (Figs. 21, 1, 22) is the remains of a carcass compressed dorsoventrally in parallel aspect. It is 87 mm long and has a maximum width of about 21 mm. Parts of the body are slightly offset laterally, especially between the seventh and eighth trunk tergites. Also, some parts of the body seem to be slightly rotated about the longitudinal axis (i.e., tilted to the horizontal or bedding surface), and effects of this on the observed configuration are difficult to assess. The parting plane passes horizontally through the body, and reflective traces of the gut and indeterminate internal features adhere to both the part and counterpart. The dorsal exoskeleton is smooth and shows no evidence of an axial lobe.

The cephalic shield is subtriangular in outline, its width being about one-third greater than its length. Posterolateral corners are rounded, and the rear margin is nearly straight. Evidence of eyes or dorsal furrows of any kind is lacking. Fine compaction wrinkles, especially common along the right-lateral edge, indicate that the shield was convex with steeper slopes along the lateral margins.

The trunk, including the telson, is about four times longer than the cephalic shield but is narrower at its anterior end. Tergites 2 and 3 may be narrower than tergite 1. Width of the trunk increases gradually from tergite 3 to about tergite 8 and decreases gradually to tergite 11. From anterior to posterior, tergites 1 to 11 approximately double in sagittal length. Posterior tergal margins are nearly straight in the anterior half of the trunk, becoming slightly concave forward on tergites 6 to 9 and then nearly straight again on tergites 10 and 11. Sharp angular terminations are evident on tergites 8 to 11. A concentration of fine compaction wrinkles on lateral ends of the tergites indicate some original convexity.

The outline of the telson is subcircular, its width being slightly greater than its length. Two pairs of tiny spines are present on the lateral margins, the anterior pair being barely discernible. The anterior end of the telson is laterally constricted, and it is the narrowest area on the dorsal exoskeleton. Width of the telson expands rearward, at a lower angle initially, and reaches a maximum just behind the midpoint at the posterior pair of spines. The posterior part of the telson is broad and semicircular with a smooth margin. A near absence of compression wrinkles suggests that the shield was flat or nearly so in the living animal.

Traces of the alimentary tract are evident in the holotype. A large irregular cluster of trilobite skeletal fragments is centered beneath the cephalic shield. These probably represent slightly scattered contents of the stomach or midgut. A narrow relective strip, offset in places, is evident through most of the trunk, terminating just behind the anterior margin of the telson. This probably represents the intestine or hindgut. Its contents, if any, are not identifiable.

A second, poorly preserved specimen (Fig. 21, 2), represented by part and counterpart, is compacted dorsoventrally in parallel aspect. With a length of 45 mm, it is about half the size of the holotype and also appears to be the remains of a carcass. Margins of the tagmata are incomplete, but preserved features closely resemble those of the holotype. The trunk shows vestiges of segmentation. A large, irregular lump beneath the cephalic shield probably represents a stomach filling, but the contents

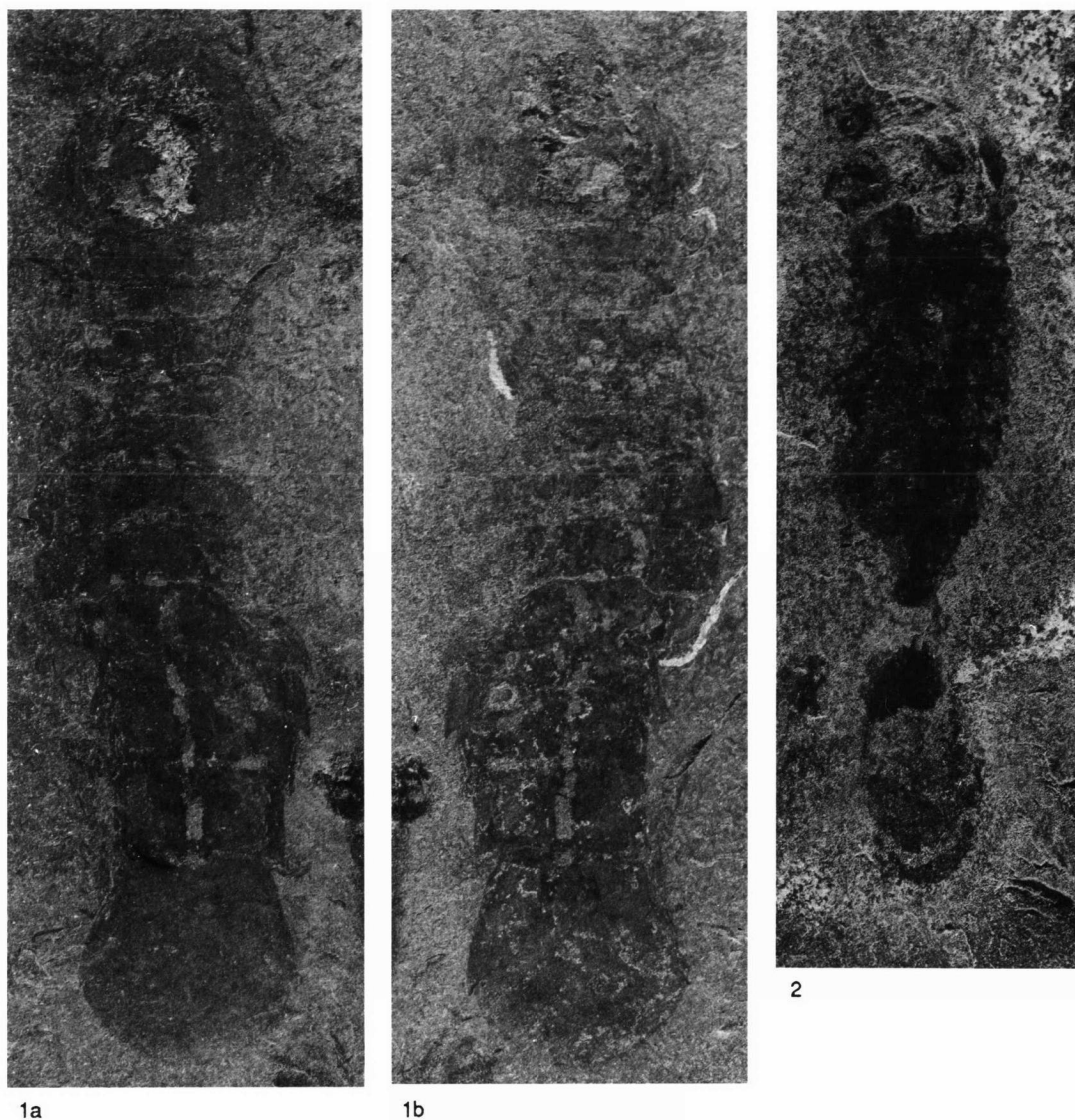


Fig. 21. *Utahcaris orion* n. gen. and n. sp. from the Spence Shale, Wellsville Mountains. —1. Holotype counterpart (a) and part (b); KUMIP 204784, $\times 1.5$. —2. Smaller specimen, part; KUMIP 204785, $\times 2.5$.

are not identifiable. Traces of a narrow gut in the trunk, in places, contain small nodules.

Discussion.—Numerous trilobite fragments preserved in the stomach of the holotype of *U. orion* indicate that the animal was a predator or scavenger. Absence of identifiable echinoderm or brachiopod fragments among the stomach contents suggests that the species was more selective in its diet than was the animal that

produced the exceptionally large coprolites described below.

A large, flat, laterally expanded telson is an unusual feature among arthropods (Plotnick and Baumiller, 1988). In outline, the telson of *U. orion* is closely convergent on that of pterygotid eurypterids. *U. orion* does not, however, show evidence of a median carina. By analogy with pterygotids, and based on func-

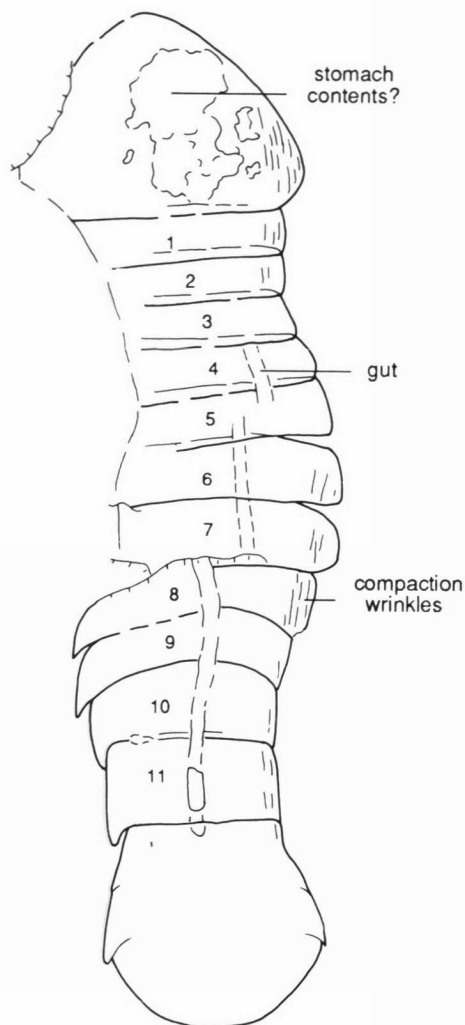


Fig. 22. *Utahcaris orion* n. gen. and n. sp., KUMIP 204784, explanatory drawing of holotype part (compare Fig. 21, 1b). Trunk tergites are numbered from the anterior.

tional interpretations by Plotnick and Baumiller (1988), the telson of *U. orion* probably served as a rudder for steering rather than as a thrust producer for propulsion. As inferred for pterygotids, *U. orion* probably was not a rapid swimmer but may have been fairly agile.

Occurrence.—Both specimens of *U. orion* are preserved in hard, medium dark-gray, flaggy parting, noncalcareous mudshale. They demonstrate a stratigraphic range through at least the upper half of the Spence Shale. The localities in Miners Hollow and Antimony Can-

yon are almost five kilometers apart on the west side of the Wellsville Mountains, Utah.

UNDETERMINED ARTHROPOD 1

Figures 23, 24

Material.—Part and counterpart of one incompletely exposed individual, KUMIP 204783, collected by Glade and Val Gunther.

Description.—The specimen is compressed dorsoventrally in parallel aspect. A cephalic shield and the anterior trunk to part of the eighth tergite are exposed. The posterior end of the body, if preserved, is concealed beneath the matrix of the counterpart. The exposed portion of the body is about 63 mm long and has a maximum width of 26 mm. The exoskeleton appears to have been smooth, but common compaction wrinkles over much of the surface suggest that it had at least moderate and probably high convexity. Evidence for a differentiated axis is equivocal. The cephalic shield is semicircular in outline, its width being about one-third greater than its length. Eyes are not present on the dorsal surface. The posterior cephalic margin bows slightly to the rear. Trunk tergites are approximately four times greater in width than length. Posterior tergite margins are irregularly bowed forward, with curvature increasing rearward.

Traces of the alimentary tract are evident along the midline of the body. A weak dark stain in the central part of the head may be related to the stomach or midgut. A narrow discontinuous trace of the hindgut commences in the rear of the head and extends through at least the sixth thoracic segment. Remnants of a reflective film are preserved in places. Some gut filling of undetermined composition stands in relief on the part and becomes separated into more distinct pelletal units toward the rear.

Discussion.—Without knowledge of the appendages and the posterior end of the body, the affinities of this specimen remain uncertain. In general body size, shape of cephalic shield, and segmentation of the thorax, it resembles some representatives of *Emeraldella* Walcott, 1912a, and *Leancoilia* Walcott, 1912a. Compared to previously described Cambrian fossils from Utah, it is most similar to *Emeraldella*? sp. Briggs and Robison, 1984, and *Leancoilia*? *hanceyi* Briggs and Robison, 1984. It appears to



Fig. 23. Undetermined arthropod 1, part (1a) and counterpart (1b) from the middle part of the Spence Shale, Wellsville Mountains; KUMIP 204783, $\times 1.5$.

differ from *Emeraldella?* sp. by having a proportionately longer cephalic shield and sagittally longer thoracic tergites. It differs from *L.?* *hanceyi* in having a semicircular rather than a subrectangular cephalic shield, and it shows no clear evidence of a differentiated axial lobe.

Occurrence.—The specimen is preserved in hard, medium-gray, flaggy parting, noncalcareous mudshale from the middle part of the Spence Shale in Miners Hollow, Wellsville Mountains, Utah.

UNDETERMINED ARTHROPOD 2

Figure 25

Material.—Counterpart of one specimen, KUMIP 204782, collected by Glenn F. Rockers.

Description.—The parting surface passes horizontally through the dorsoventrally compressed body, mostly exposing internal fea-

tures. The head region is trapezoidal in outline, its maximum width being about twice its sagittal length. Lateral margins of the head taper forward moderately, bending rather abruptly as they pass into a blunt, nearly straight, frontal margin. A pair of small dark spots just inside the anterolateral corners of the head may indicate eye positions. A long trunk region tapers rearward at a gradually increasing rate. An irregular, dark, slightly tapering trace runs along the axis of the specimen for most of its length and presumably represents the alimentary tract and perhaps associated organs. In low, oblique light (Fig. 25, 1b), the alimentary canal is indicated by a narrow groove, which anteriorly and posteriorly retains remnants of a filling of unidentified composition. Lateral extensions of the dark axial trace appear to be segmentally arranged (Fig. 25, 1a). Although

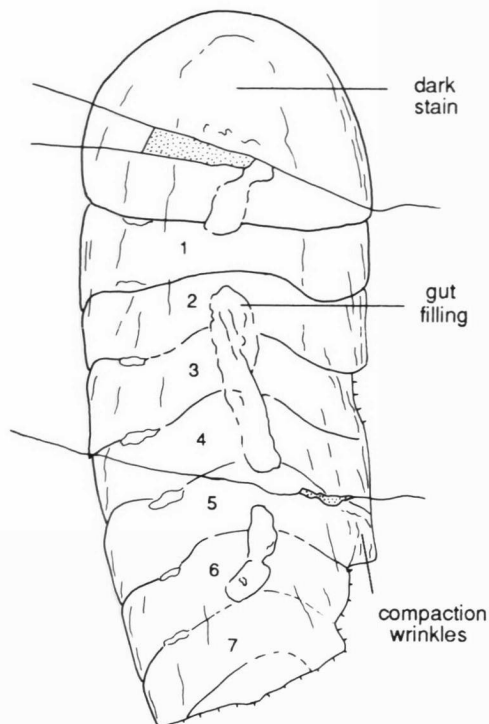


Fig. 24. Undetermined arthropod 1, KUMIP 204783, explanatory drawing of part (compare Fig. 23, 1a). Trunk tergites are numbered from the anterior.

features become less clear toward the rear, the trunk appears to have at least 10 or 11 somites. Weak traces in pleural areas of the trunk may be vestiges of appendages.

Discussion.—Compared to arthropods from the Burgess shale, this specimen most closely resembles those of *Actaeus armatus* Simonetta, 1970, and *Alalcomenaeus cambricus* Simonetta, 1970, which are few, poorly known, and possibly synonymous (Briggs and Robison, 1984: 16). The bodies are similar in form and the number of trunk somites may be the same. Shape of the anterior cephalic margin differs, but that may be the result of taphonomic factors. The anterior end of the cephalic shield in the single known specimen of *A. armatus* is poorly defined but has a pair of suboval areas thought to be eye lobes (Whittington, 1981: 349, figs. 110–114). Compression of such lobes across the anterior margin could have produced the different outline seen here. Without more

knowledge of anatomy, however, the identity of this Utah specimen remains undetermined.

Dark stains are commonly associated with some fossils of the Burgess shale, mostly around the posterior end of the body, and are thought to have been produced by seepage of body contents during the initial stages of decay (Conway Morris, 1977b:625–626; Whittington, 1985:35–36). Two superimposed stains of different size and color are present on matrix surrounding the head of this Utah fossil (Fig. 25, 1a). They are subcircular and are approximately concentric about the inferred position of the mouth. The preservation of the stains suggests rapid burial followed by either differential diffusion of staining agents during one seepage event or unequal seepage during two events.

Occurrence.—The specimen is preserved in laminated, medium dark-gray, lime mudstone from locality 347 in the lower Marjum Formation of the House Range, Utah. A diverse biota identified from the same locality has been listed by Briggs and Robison (1984:5–6).

Phylum, Class, and Order uncertain

Family Anomalocarididae Raymond, 1935

Genus ANOMALOCARIS Whiteaves, 1892

ANOMALOCARIS NATHORSTI (Walcott, 1911a)

Figure 26

New material.—Part and counterpart of one, small, incomplete cephalic appendage, KUMIP 204781, which was collected by Lloyd Gunther. Also, four isolated blades from cephalic appendages, KUMIP 204777–204780; three being represented by part and counterpart. Three of the isolated blades were collected by Lloyd and Val Gunther and one was collected by Robert and Nancy Meyers.

Description.—The incomplete cephalic appendage (Fig. 26, 3) is laterally compressed and is indifferently preserved. It seems to retain all but two or three of the proximal podomeres. Some of its long blades overlap and are compacted. Spines are not evident on the blades, but they may be covered or not be preserved.

The four isolated appendage blades are preserved as lateral compressions (e.g., Fig. 26, 1, 2). Each blade terminates distally in two long spines of similar size. Other spines vary in length along one margin of the blade.

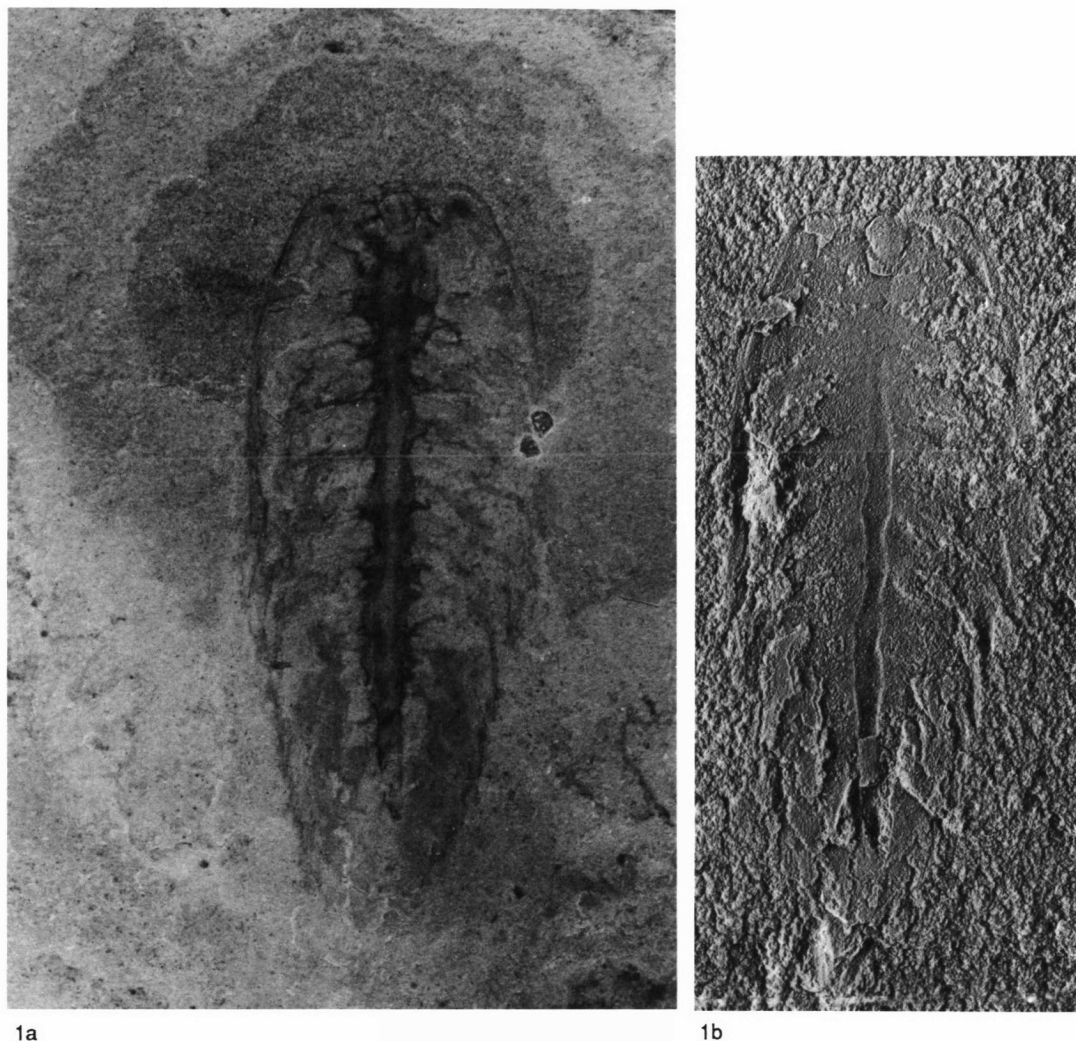


Fig. 25. Undetermined arthropod 2 from the Marjum Formation, House Range; KUMIP 204782, $\times 3$.—1a. Counterpart showing internal features and two superimposed dark stains on matrix about the head.—1b. Same specimen lightly coated with magnesium oxide and photographed in low oblique light to show gut trace, anterior and posterior remnants of gut filling, and weak segmentation.

Discussion.—The new specimens from Utah closely resemble some from British Columbia that were described and illustrated by Briggs (1979) as ‘Appendage F’ of *Anomalocaris*? and which subsequently were reassigned to *Anomalocaris nathorsti* (Walcott, 1911a) by Whittington and Briggs (1985; see for terminology used here). Although relatively small, the new incomplete appendage (Fig. 26,3) has overlap-

ping and compacted blades, a feature that has been noted as characteristic of specimens in the Burgess shale (Briggs, 1979:645). It also seems to retain about the same number of podomeres and is preserved in a position similar to that of an incomplete appendage illustrated from the Burgess (Briggs, 1979, pl. 80, fig. 3; text-fig. 22). The new isolated blades are not disarticulated at their bases (e.g., Fig. 26,1,2) but are

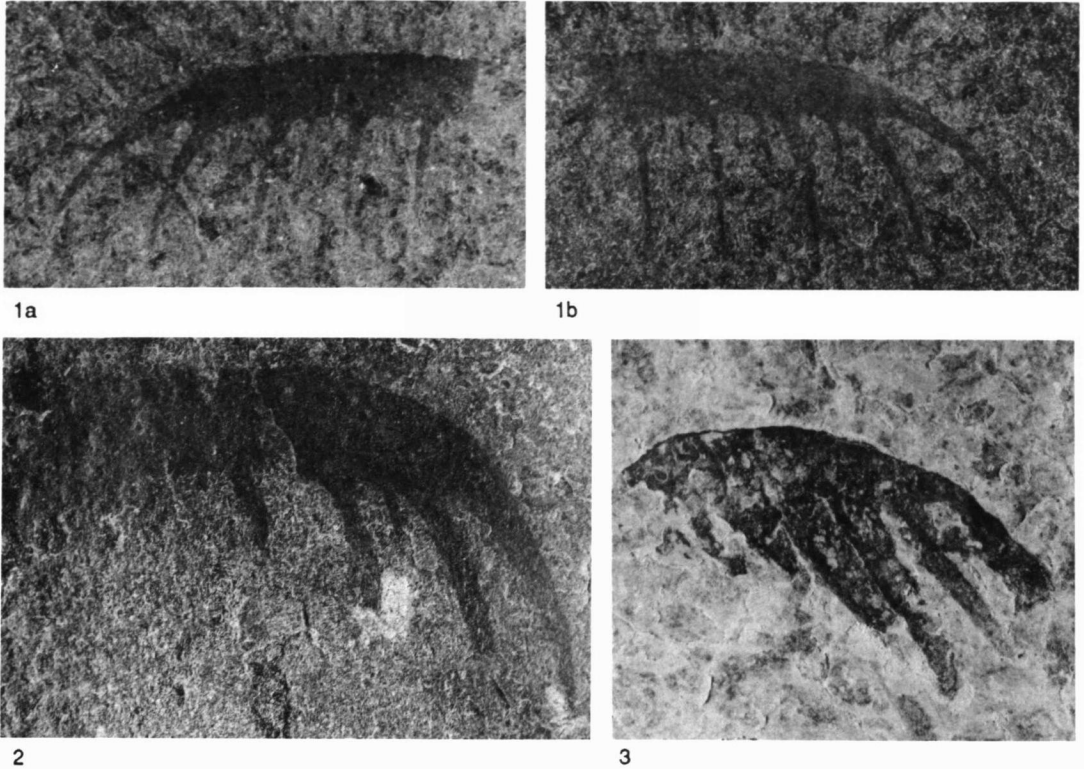


Fig. 26. *Anomalocaris nathorsti* (Walcott), all $\times 4$.—1, 2. Isolated blades from cephalic appendages (1a,b, part and counterpart); unnumbered localities, upper Spence Shale, Antimony Canyon, Wellsville Mountains; KUMIP 204777 and 204778, respectively.—3. Incomplete cephalic appendage; locality 114, Wheeler Formation, House Range; KUMIP 204781.

broken along the blade, also a feature noted as being characteristic of blades in the Burgess shale (Briggs, 1979:645, pl. 81, figs. 6, 7).

Previous reports of *A. nathorsti* from Utah were based on two jaw structures (then interpreted as the medusoid *Peytoia*) from the Wheeler Formation (Conway Morris and Robison, 1982) and the posterior portion of an entire animal from the Marjum Formation (Briggs and Robison, 1984), all from the House Range. Although isolated appendages of *Anomalocaris* are well known from Lower and Middle Cambrian localities throughout western North America (Briggs, 1979; Briggs and Mount, 1982; Collins, Briggs, and Conway Morris, 1983; Whittington and Briggs, 1985), these are the first remains of such appendages to be reported from Utah. Some fossils in the Spence Shale that superficially resemble the jaw struc-

ture of *Anomalocaris* (Conway Morris and Robison, 1982:120–121, pl. 1, fig. 6) are here assigned to the alga *Acinocricus stichus* n. gen. and n. sp.

In discussing the stratigraphic range of *Anomalocaris*, it is also worth noting a newly recognized relative from the Lower Cambrian of Poland. A single specimen of the supposed arthropod *Cassubia infercambriensis* (Lendzion, 1975, 1977) from a subsurface core of the Zawiszany Formation was reclassified as an anomalocarid by Dzik and Lendzion (1988), although these authors opted to retain the name *Cassubia* rather than transferring the specimen to *Anomalocaris*. However, based on examination of the specimen by one of us (SCM) in Uppsala in 1986 (courtesy of Dr. Kazimiera Lendzion), placement in *Anomalocaris* would seem possible. In any case, this occurrence is of

particular interest because of associated *Mobergella*, which might indicate a correlation with the upper part of the Tommotian Stage (Bengtson, 1977), although Dzik and Lendzion (1988) argued for correlation with the overlying Attabanian Stage.

Occurrence.—The four isolated appendage blades are preserved in hard, grayish-olive to medium dark-gray, flaggy parting, noncalcareous mudshale. Three are from the middle and upper Spence Shale in Antimony Canyon, and one is from the upper Spence Shale in Miners Hollow, all from the Wellsville Mountains, Utah. These are the first *Anomalocaris* to be reported from the Spence Shale. The incomplete appendage is preserved in soft, laminated, light-gray, lime mudstone from locality 114 in the Wheeler Formation of the House Range, Utah. Locality 114 has previously produced two jaw structures similar to those of *A. nathorsti* (Conway Morris and Robison, 1982; see also Briggs and Robison, 1984:5).

Family ELDONIIDAE Walcott, 1911b

Genus ELDONIA Walcott, 1911b

This genus was erected by Walcott (1911b) for medusiform organisms from the phyllopod bed of the Burgess shale. Apparent restriction to a specific horizon (Walcott, 1911b, 1912a; Conway Morris, 1976) could reflect the entrapment of a shoal of these animals. Walcott (1911b) regarded *Eldonia* as a holothurian, and although this assignment was accepted by neither Clark (1912) nor Madsen (1956, 1957, 1962), such a relationship was reaffirmed by Durham (1974), who reviewed the history of research. More recently, Paul and Smith (1984) have expressed renewed scepticism that *Eldonia* is a holothurian. Pending a systematic reexamination of available material, the higher taxonomic affinities of this genus are best regarded as uncertain.

ELDONIA LUDWIGI Walcott, 1911b

Figures 27–29

New material.—Two specimens have been collected in Utah. One (KUMIP 204370), a part only, was collected by Lloyd and Val Gunther from the middle part of the Spence Shale in Antimony Canyon of the Wellsville



Fig. 27. *Eldonia ludwigi* Walcott, KUMIP 204370, associated with *Haplophrentis reesei* Babcock and Robison (upper center) and *Ctenocystis utahensis* Robison and Sprinkle (upper right); from upper Spence Shale, locality 781, Wellsville Mountains, $\times 2$.

Mountains. The other (KUMIP 204371), part and counterpart, was collected by Frieda and Lloyd Gunther at locality 811 in the middle Marjum Formation of the House Range.

Description.—Although the specimen from the Spence Shale (Fig. 27) is indifferently preserved, it appears to be conspecific with the material from the phyllopod bed of the Burgess shale. It is incomplete but probably had a diameter of about 40 mm. The curved intestine is clearly visible and, as in specimens from the phyllopod bed, is now composed of a strongly reflective film. However, neither the extensions towards the foregut and feeding tentacles nor the hindgut are clearly preserved. Probably these latter regions had relatively thin walls in

comparison with the more robust, possibly muscular midgut and hence were more prone to decay (cf. Walcott, 1911b:49). Dark areas on either side of the midgut crudely define the original medusoid shape but do not preserve such internal structures as the canals and mesenteries that are present in specimens from the phyllopod bed (Walcott, 1911b; Durham, 1974). The outer region, however, is radially divided into zones that presumably correspond to the exumbrellar lobes discussed by Walcott (1911b, see especially his pl. 11, figs. 1, 2).

The new specimen from the Marjum Formation (Figs. 28, 29) is relatively large. Its intestine is well preserved, but the traces of its medusiform body show little discernible detail except for possible remnants of the radiating mesenterial system imposed on the intestine. Specimens from the Burgess shale show a wide range in size, and the variation in specimens described here falls within the observed limits.

Occurrence.—*E. ludwigi* has previously been recorded only from the *Ptychagnostus praecurrens* Zone at the Burgess shale locality in British Columbia. These new specimens extend the observed stratigraphic range of the species in North America through much of the Middle Cambrian, from the *Peronopsis bonnerensis* Zone (middle Spence Shale) to the *Ptychagnostus punctuosus* Zone (middle Marjum Formation). Its observed geographic range is extended about 1300 km from British Columbia to Utah.

Supposed scyphozoans from the Chiungchussu Formation of Early Cambrian age (*Eoredlichia-Wutingaspis* Zone) in eastern Yunnan, China, may also be referred to *Eldonia*. In particular, the medusiform *Stellostomites eumorphus* Sun and Hou (1987a, pl. 4, figs. 1-6; pl. 5, figs. 1, 2; text-figs. 5, 6) shows clear evidence for the prominent intestine according to an examination by one of us (SCM). In addition, *Yunnanomedusa eleganta* Sun and Hou (1987a, pl. 6, figs. 1, 2; text-fig. 7) is also interpreted as synonymous with *Eldonia*. Thus, these Atdabanian occurrences of *Eldonia*, like those of *Naraoia* and *Anomalocaris*, confirm the remarkable stratigraphic durations of some taxa of the Burgess shale.

Of related interest, another supposed medusoid from the Chiungchussu Formation was also wrongly assigned. *Heliomedusa orienta*, which was assigned to the Hydrozoa by Sun

and Hou (1987a, pl. 1, figs. 1-13; pl. 2, figs. 1-11; text-figs. 2, 3; see also Hou and Sun, 1988, pl. 4, figs. 1-5), is here regarded as a thin-shelled brachiopod. One of us (SCM) has examined the illustrated specimens, and the supposed marginal tentacles appear to represent mantle setae. These, together with a bivalve condition and presence of possible shell structure, support our conclusion.

Family WIWAXIIDAE Walcott, 1911c

Genus WIWAXIA Walcott, 1911c

Type (and only known) species.—*Orthotheca corrugata* Matthew, 1899, p. 42, pl. 1, fig. 3; by original designation (Walcott, 1911c:123).

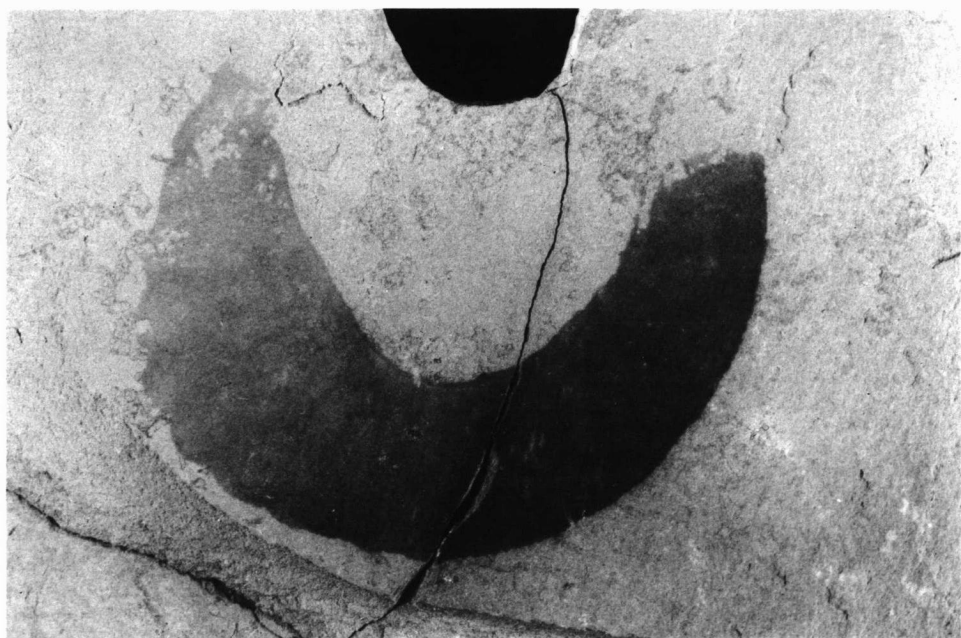
Discussion.—This lepidote metazoan was first described by Matthew (1899) on the basis of an isolated spine from the *Ogygopsis* shale, a prolifically fossiliferous horizon within the lower part of the Stephen Formation. Although Matthew (1899) misidentified the specimen as a hyolith tube, discovery of articulated material in the phyllopod bed at the nearby Burgess shale locality demonstrated that the original organism bore a series of scales and spines (Walcott, 1911b, 1931), collectively referred to as sclerites. A detailed restudy by Conway Morris (1985a) documented the distribution of the various types of sclerites across the body, so that several distinct zones can be recognized. The affinities of *Wiwaxia* remain uncertain, but on the basis of a radular structure in the foregut and other general anatomical similarities, a distant relationship with the Mollusca was proposed.

Hitherto, *Wiwaxia* has been recorded only from the Stephen Formation of British Columbia. An extensive suite of specimens from the phyllopod bed at the Burgess shale locality is supplemented by mostly disarticulated material from another four nearby localities. In total, it suggests that *Wiwaxia* may have ranged through a substantial part of the Stephen Formation (Collins, Briggs, and Conway Morris, 1983; Conway Morris, 1985a).

As the sclerites were inserted separately onto the body, on death they normally would have dispersed. Evidence also indicates that the animal periodically molted its scleritome during growth (Conway Morris, 1985a), and some sclerites probably became isolated by this



1a



1b

Fig. 28. *Eldonia ludwigi* Walcott, part (1a) and counterpart (1b) from the middle Marjum Formation, locality 811, House Range; KUMIP 204371, $\times 2$.

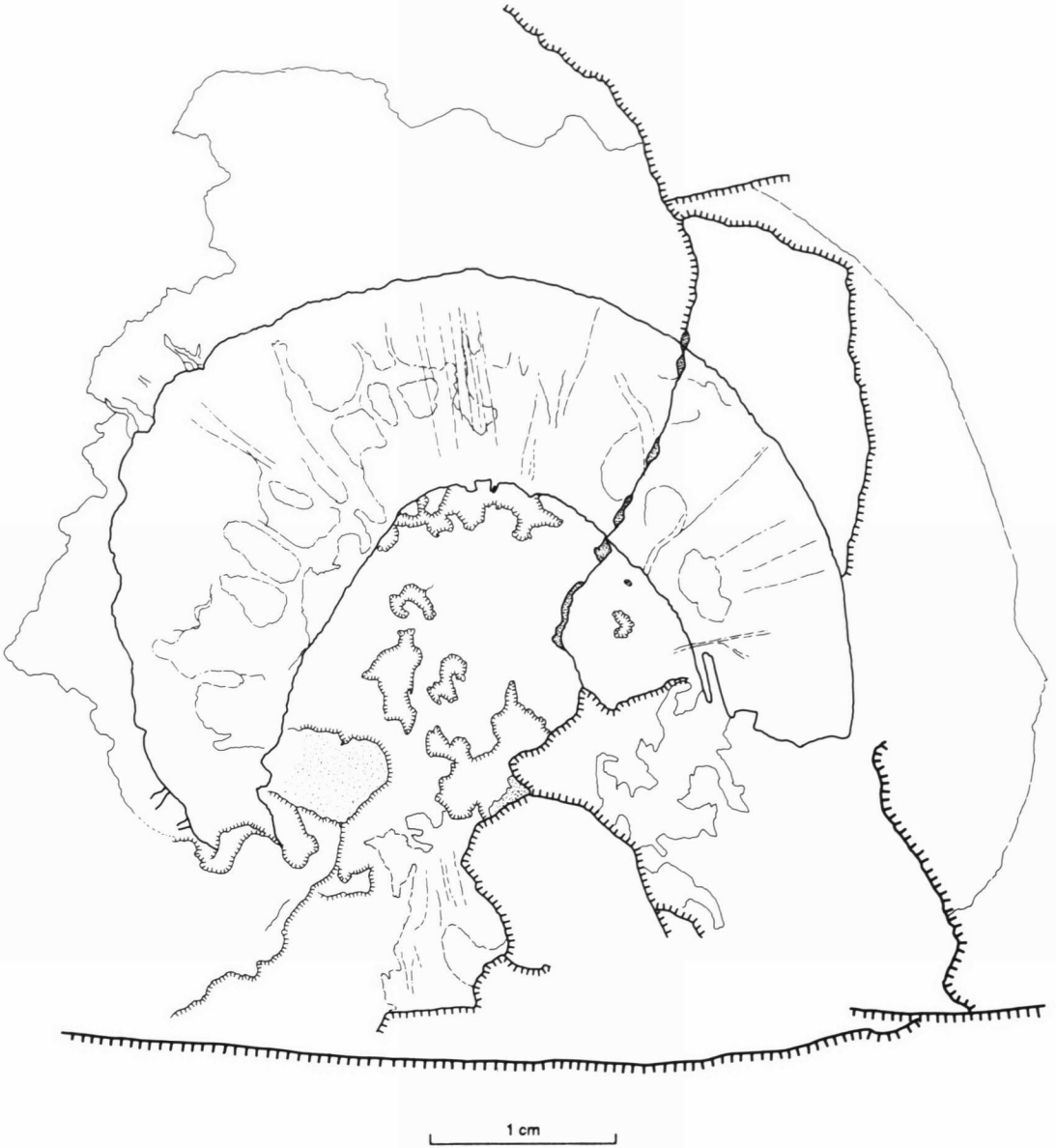


Fig. 29. *Eldonia ludwigi* Walcott, KUMIP 204371, explanatory drawing of part with some features of counterpart transferred by reversal (compare Fig. 28, 1a, b).

mechanism. Articulated specimens evidently owe their preservation to rapid burial during catastrophic events, but even where the scleritome broke up after death it seems likely that the isolated sclerites probably had a moderate residence time in the sediment before ultimate destruction by microbial activity. Thus, in fa-

vorable circumstances the isolated sclerites were fossilized.

WIWAXIA sp. cf. W. CORRUGATA
(Matthew, 1899)

Figure 30

New material.—Two isolated sclerites, a scale

(KUMIP 204367) and a spine (KUMIP 204366), were collected by Lloyd Gunther from the Spence Shale at locality 718 in the Wellsville Mountains, Utah. They are preserved in hard, flaggy parting, medium dark-gray, noncalcareous mudshale. On the parting surface with the scale is a large shell of the articulate brachiopod *Wimanella* sp.

Description.—The isolated scale (Fig. 30,2) has a short extension at its proximal end, probably representing part of the root that originally was inserted in the body wall. Faintly reflective longitudinal lines represent ribbing, which characterizes all sclerites of *W. corrugata*. A symmetrical shape demonstrates that it was probably located on the lateral region of the body, whereas its elongation suggests that it derives from the lower lateral rather than upper lateral region (see Conway Morris, 1985a, fig. 168).

The other specimen (Fig. 30,1) is more poorly preserved, but clearly is one of the spinose sclerites. Articulated material of *W. corrugata* demonstrates that the animal bore a row of prominent spines along each of its dorsolateral margins (Conway Morris, 1985a, fig. 171), and this spine presumably occupied a comparable position.

Discussion.—These new sclerites are indistinguishable from those of *W. corrugata* and probably are conspecific. Experience with the study of sclerites from the Lower Cambrian, however, demonstrates that although particular isolated sclerites of some species are indistinguishable, when a large enough sample is available, systematic differences may become apparent. Accordingly, pending the discovery of an extensive suite of isolated sclerites or, preferably, articulated individuals with an intact scleritome, we deem it prudent to refer this new material from the Spence Shale to *Wiwaxia* sp. cf. *W. corrugata*.

With respect to polymeroid trilobite biostratigraphy (Robison, 1976), *W. corrugata* has an observed stratigraphic range in the Stephen Formation from the upper *Glossopleura* Zone to the lower *Bathyriscus-Elrathina* Zone. The new sclerites from the Spence Shale are associated with a fauna that is representative of the upper *Glossopleura* Zone. Therefore, they probably do not extend the observed stratigraphic range of *Wiwaxia*, but they do extend its observed geographic range by about 1200 km.

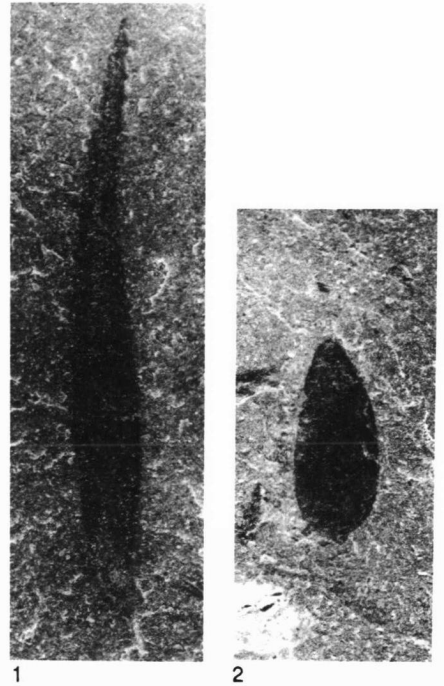


Fig. 30. *Wiwaxia* sp. cf. *W. corrugata* (Matthew) from the Spence Shale, Wellsville Mountains, Utah.—1. Isolated spine from dorsolateral row; KUMIP 204366, $\times 5$.—2. Isolated scale, probably from lateral part of scleritome; KUMIP 204367, $\times 5$.

Like many soft-bodied taxa that are best known from the Burgess shale, the scarcity of *W. corrugata* is probably more a reflection of unsuitable preservation conditions than of restricted distribution. Thus, the observed geographic and stratigraphic ranges may be seriously incomplete. *W. corrugata* is believed to be closely related to the Halkieriidae, a family characterized by calcified sclerites that as fossils are typically replaced by diagenetic phosphate (Bengtson and Conway Morris, 1984). With one possible exception, the halkieriids are not presently known in strata younger than the Atdabanian Stage of the Lower Cambrian (roughly equivalent to the *Fallotaspis* Zone as used in North America; see Fritz, 1972). Therefore, the apparent stratigraphic gap between the last halkieriids and first wiwaxiids is equivalent to much of the Lower Cambrian and basal Middle Cambrian. Halkieriid sclerites are routinely extracted by acid digestion of carbonate matrix because the secondary phos-

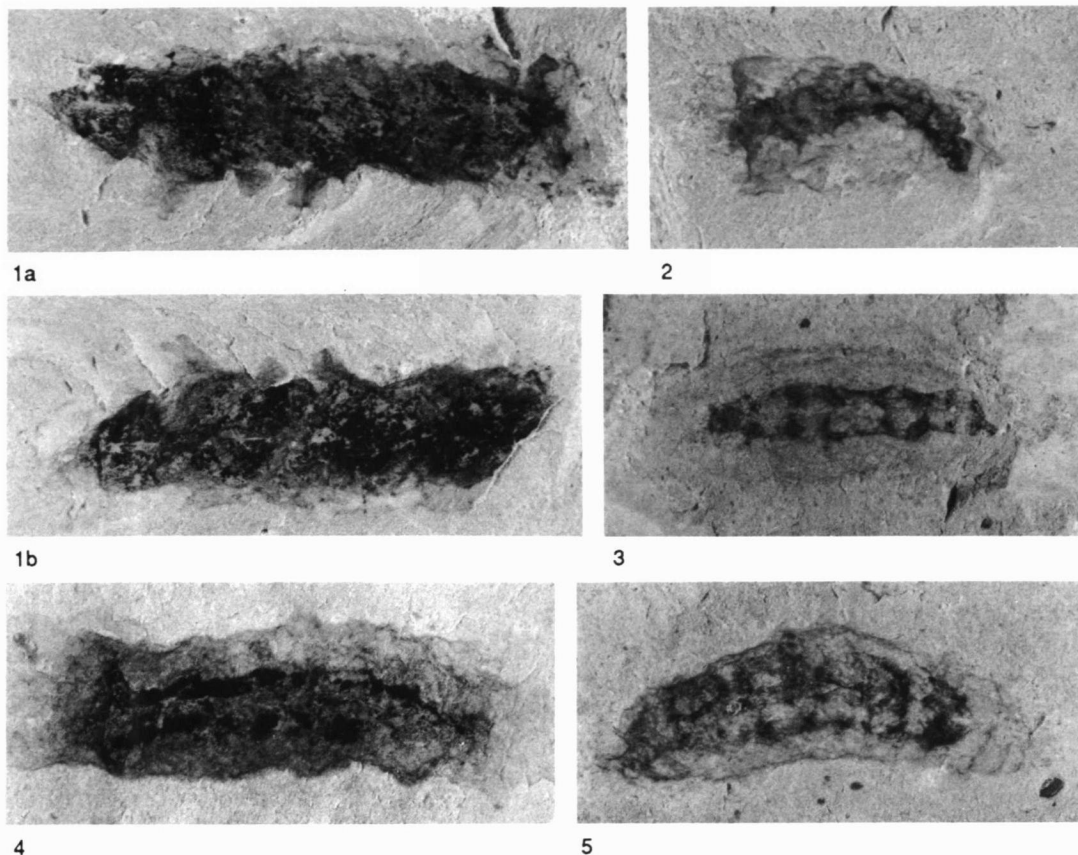


Fig. 31. Undetermined worms from the upper Wheeler Formation at locality 116 in the House Range, Utah; all $\times 3$.—1a,b. Part and counterpart, USNM 424115, with parapodia-like extensions on one side.—2. USNM 424116.—3. USNM 424117 with dark, well-defined, medial trace probably representing gut.—4,5. USNM 424118 and 424119, respectively.

phate of the sclerites is more or less insoluble. Although diagenetic phosphatization is prevalent in the lowest Cambrian rocks, unaltered halkieriid sclerites may be easily overlooked on account of their small size. A number of Lower Cambrian localities with soft-bodied fossils are known (e.g., Kinzers Formation of Pennsylvania, Emu Bay Shale of South Australia, Buen Formation of North Greenland), but none has produced either halkieriids or wiwaxiids. Therefore, until further information becomes available, the evolutionary history of the halkieriids and wiwaxiids will probably remain largely speculative.

UNDETERMINED WORMS

Figure 31

Material.—Almost 100 specimens were collected by Lloyd, Metta, and Val Gunther at locality 116 in the upper Wheeler Formation of the House Range, Utah. These and many associated fossils are deposited at the U.S. National Museum of Natural History (accession number 368342). Most are preserved in soft, laminated, medium light-gray, argillaceous, lime mudstone. Among several associated taxa, representatives of the agnostoid trilobite *Peronopsis interstricta* (White) and the

stylophoran echinoderm *Cothurnocystis?* *bifida* Ubachs and Robison are especially common.

Description—Typically the specimens are vermiform with a relatively low length to width ratio. A prominent broad strand of dark material may represent the alimentary canal (Fig. 31). In some specimens the strand shows evidence of segmentation (Figs. 31, 2, 3, 5). This dark area may occupy most of the visible specimen (Fig. 31, 1*a*, 1*b*, 4) or be flanked by a body (Fig. 31, 2, 3, 5) that may itself show signs of segmentation. In some specimens lobate extensions are also evident (Fig. 31, 1*a*, 1*b*).

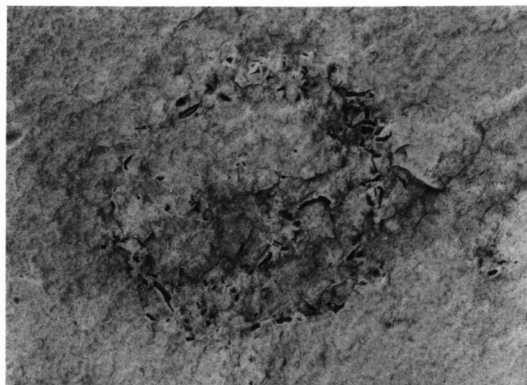
Discussion.—The affinities of these specimens are problematic, and it would be unwise to assume that they all represent one taxon.

COPROLITES

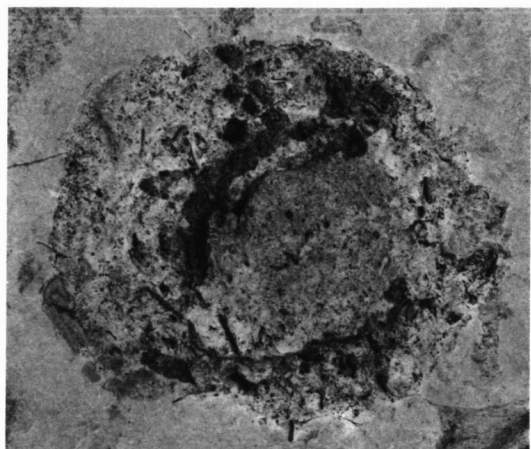
Figure 32

Cambrian coprolites have received little attention. In a search of 376 publications on coprolites, Häntzschel, El-Baz, and Amstutz (1968) could find no description of either a Precambrian or a Cambrian coprolite. Actually, a fecal origin has commonly been cited, but not especially emphasized, for pellets that may be rare to abundant in some Cambrian limestones and shales (e.g., Bentley, 1958). Most larger coprolites at some Cambrian localities have been overlooked or ignored. As an exception, Sprinkle (1973:100, pl. 21, fig. 7) briefly described and illustrated a distinctive type of large coprolite from the Stephen Formation of Alberta, Canada, filled with skeletal fragments of trilobites and echinoderms. In addition, he reported occurrences of similar coprolites at other Cambrian localities in the Rocky Mountains. A similar fossil, which came from a bed with many trilobites and echinoderms, was described and illustrated from the Marjum Formation of the House Range by Conway Morris and Robison (1986:20, fig. 10, 2). Additional specimens from the Spence Shale of northern Utah, described here, provide more information about the food preferences and possible size of their producers.

Large, round, compressed coprolites locally are common in the Spence Shale. As in the Stephen Formation (Sprinkle, 1973), most of these are between about 25 and 30 mm in diameter (e.g., Fig. 32, 1), but they have an observed range to about 45 mm (Fig. 32, 2).



1



2

Fig. 32. Coprolites from the Spence Shale, Wellsville Mountains; both containing skeletal plates of ctenocystoids and eocrinoids, sclerites of trilobites, and shells of inarticulate brachiopods. —1. Typical specimen on bedding surface from locality 101; small holes are mostly solution casts of echinoderm plates; KUMIP 204368, $\times 1.3$. —2. Largest observed specimen, locality 781; KUMIP 204369, $\times 1.3$.

Texture of the groundmass closely resembles that of surrounding matrix, but the coprolite usually is browner because of its higher organic content. Large inclusions vary in abundance and consist almost entirely of skeletal or shell material of trilobites, echinoderms, and brachiopods. The dominant kind of skeletal or shelly inclusion usually corresponds to the taxon that is most commonly represented on the surrounding bedding surface. Thus, the coprolite producers must have been either predators or scavengers, and they seem to have been oppor-

tunists that fed rather indiscriminately on associated animals with hard parts. Presumably they also fed on available soft-bodied animals, but these have left no identifiable remains in the coprolites.

The coprolites are of considerable size relative to that of any associated body fossil. Moreover, since the coprolites lacked a rigid covering, it is unlikely that their size was appreciably increased by lateral expansion during postdepositional compression (see general explanation by Briggs and Williams, 1981). According to Whittington and Briggs (1985), the largest animal known from Cambrian rocks is *Anomalocaris*, an inferred predator. From the largest isolated appendages, they estimated that the animal may have attained a length of about 0.5 m. It may be pertinent to this discussion that *Anomalocaris* is present through much of the Cambrian System, including both the Stephen Formation and the Spence Shale. Upward scaling of observed gut traces from available specimens of *Anomalocaris* (Briggs and Robison, 1984; Whittington and Briggs, 1985) suggests that an individual about 0.5 m in length probably had a maximum gut diameter of no more than about 20 mm. The gut of *Anomalocaris* tapers toward the rear, however, and the terminal maximum diameter may have been no more than about 10 mm. An unknown expansion limit for such a gut as well as that of the anal sphincter makes dubious any estimate of related feces diameter. Nevertheless, a coprolite 45 mm in diameter suggests that the producer may have been either an *Anomalocaris* much larger than previously imagined or an unidentified predator or scavenger substantially larger than *Anomalocaris*.

REFERENCES

- Andrews, H. N., Jr. 1961. Studies in Paleobotany. John Wiley & Sons (New York). 487 p.
- Babcock, L. E., and R. M. Feldmann. 1986. The phylum Conulariida, p. 135-147. In Antoni Hoffman and M. H. Nitecki (eds.), Problematic Fossil Taxa. Oxford University Press (New York).
- , and R. A. Robison. 1988. Taxonomy and paleobiology of some Middle Cambrian hydrozoans (Cnidaria) and hyoliths (Mollusca) from western North America. University of Kansas Paleontological Contributions, Paper 121.
- Bengtson, Stefan. 1977. Aspects of problematic fossils in the early Palaeozoic. Acta Universitatis Upsaliensis 415:1-71.
- , and Simon Conway Morris. 1984. A comparative study of Lower Cambrian *Halkieria* and Middle Cambrian *Wiwaxia*. Lethaia 17:307-329.
- Bentley, C. B. 1958. Upper Cambrian stratigraphy of western Utah. Brigham Young University Research Studies 5(6):1-70.
- Bold, H. C., and M. J. Wynne. 1985. Introduction to the Algae (2nd edition). Prentice-Hall, Inc. (Englewood Cliffs, New Jersey). 720 p.
- Briggs, D. E. G. 1979. *Anomalocaris*, the largest known Cambrian arthropod. Palaeontology 22:631-664.
- , and Desmond Collins. In press. A Middle Cambrian chelicerate from Mount Stephen, British Columbia. Palaeontology 31.
- , and Simon Conway Morris. 1986. Problematica from the Middle Cambrian Burgess shale of British Columbia, p. 167-183. In Antoni Hoffman and M. H. Nitecki (eds.), Problematic Fossil Taxa. Oxford University Press (New York).
- , and J. D. Mount. 1982. The occurrence of the giant arthropod *Anomalocaris* in the Lower Cambrian of California and the overall distribution of the genus. Journal of Paleontology 56:1112-1118.
- , and R. A. Robison. 1984. Exceptionally preserved nontrilobite arthropods and *Anomalocaris* from the Middle Cambrian of Utah. University of Kansas Paleontological Contributions, Paper 111:1-23.
- , and H. B. Whittington. 1985. Modes of life of arthropods from the Burgess shale, British Columbia. Transactions of the Royal Society of Edinburgh 76: 149-160.
- , and S. H. Williams. 1981. The restoration of flattened fossils. Lethaia 14:157-164.
- Bruton, D. L., and H. B. Whittington. 1983. *Emeraldella* and *Leancoilia*, two arthropods from the Burgess shale, Middle Cambrian, British Columbia. Philosophical Transactions of the Royal Society of London (B) 300: 553-585.
- Clark, H. L. 1912. Fossil holothurians. Science 35: 274-278.
- Collins, Desmond. 1986. Paradise revisited. Rotunda 19: 30-39.
- , D. E. G. Briggs, and Simon Conway Morris. 1983. New Burgess shale fossil sites reveal Middle Cambrian faunal complex. Science 222:163-167.
- Conway Morris, Simon. 1976. A new Cambrian lophophore from the Burgess shale of British Columbia. Palaeontology 19:199-222.
- , 1977a. Fossil priapulid worms. Special Papers in Palaeontology 20:1-95.
- , 1977b. A new metazoan from the Cambrian Burgess shale of British Columbia. Palaeontology 20: 623-640.
- , 1978. *Selkirkia* Walcott, 1911 (Priapulida): proposed designation of a type-species under the plenary powers, Z. N. (S.) 2171. Bulletin of Zoological Nomenclature 35:49-50.
- , 1985a. The Middle Cambrian metazoan *Wiwaxia corrugata* (Matthew) from the Burgess shale and *Ogygopsis* shale, British Columbia, Canada. Philosophical Transactions of the Royal Society of London (B) 307: 507-586.
- , 1985b. Cambrian lagerstätten: their distribution and significance. Philosophical Transactions of the Royal Society of London (B) 311:49-65.

- . 1986. The community structure of the Middle Cambrian phyllopod bed (Burgess shale). *Palaeontology* 29:423-467.
- , J. S. Peel, A. K. Higgins, N. J. Soper, and N. C. Davis. 1987. A Burgess shale-like fauna from the Lower Cambrian of North Greenland. *Nature* 326:181-183.
- , and R. A. Robison. 1982. The enigmatic medusoid *Peytoia* and a comparison of some Cambrian biotas. *Journal of Paleontology* 56:116-122.
- , and ———. 1986. Middle Cambrian priapulids and other soft-bodied fossils from Utah and Spain. *University of Kansas Paleontological Contributions*, Paper 117:1-22.
- , and H. B. Whittington. 1985. Fossils of the Burgess shale: a national treasure in Yoho National Park, British Columbia. *Geological Survey of Canada, Miscellaneous Report* 43:1-31.
- Dixon, P. S. 1970. A critique of the taxonomy of marine algae. *Annals of the New York Academy of Sciences* 175(2):617-622.
- Durham, W. J. 1974. Systematic position of *Eldonia ludwigi* Walcott. *Journal of Paleontology* 48:750-755.
- Dzik, Jerzy, and Kazimiera Lendzion. 1988. The oldest arthropods of the East European platform. *Lethaia* 21:29-38.
- Feldmann, R. M., and L. E. Babcock. 1986. Exceptionally preserved conulariids from Ohio—reinterpretation of their anatomy. *National Geographic Research* 2:464-472.
- Fritz, W. H. 1971. Geological setting of the Burgess shale, p. 1155-1170. In E. L. Yochelson (ed.), *Proceedings of the North American Paleontological Convention*, 1969, Chicago, vol. 2. Allen Press (Lawrence).
- . 1972. Lower Cambrian trilobites from the Sekwi Formation type section, Mackenzie Mountains, north-western Canada. *Geological Survey of Canada, Bulletin* 212:1-90.
- Fry, W. L. 1983. An algal flora from the Upper Ordovician of the Lake Winnipeg region, Manitoba, Canada. *Review of Palaeobotany and Palynology* 39:313-341.
- , and H. P. Banks. 1955. Three new genera of algae from the Upper Devonian of New York. *Journal of Paleontology* 29:37-44.
- Goldstein, Melvin, and Susan Morrall. 1970. Gametogenesis and fertilization in *Caulerpa*. *Annals of the New York Academy of Sciences* 175(2):660-672.
- Gunther, L. F., and V. G. Gunther. 1981. Some Middle Cambrian fossils of Utah. *Brigham Young University Geology Studies* 28(1):1-81.
- Häntzschel, Walter. 1962. Trace fossils and problematica, p. W177-W245. In R. C. Moore (ed.), *Treatise on Invertebrate Paleontology*, Part W, Miscellaneous. Geological Society of America and University of Kansas Press (New York and Lawrence).
- . 1975. Trace fossils and problematica. *Treatise on Invertebrate Paleontology*, Part W, Supplement 1, Curt Teichert (ed.). Geological Society of America and University of Kansas (Boulder and Lawrence). 269 p.
- , Farouk El-Baz, and G. C. Amstutz. 1968. Coprolites, an annotated bibliography. *Geological Society of America, Memoir* 108:1-132.
- Hillis-Colinvaux, Llewellya. 1984. Systematics of the Siphonales, p. 271-296. In D. E. G. Irvine and D. M. John (eds.), *Systematics of the Green Algae*. Systematics Association Special Volume No. 27. Academic Press (London and Orlando).
- Hou Xian-guang. 1987a. Two new arthropods from Lower Cambrian, Chengjiang, eastern Yunnan [in Chinese, with English summary]. *Acta Palaeontologica Sinica* 26:236-256.
- . 1987b. Three new large arthropods from Lower Cambrian, Chengjiang, eastern Yunnan [in Chinese, with English summary]. *Acta Palaeontologica Sinica* 26:272-285.
- . 1987c. Early Cambrian large bivalved arthropods from Chengjiang, eastern Yunnan [in Chinese, with English summary]. *Acta Palaeontologica Sinica* 26:286-298.
- , and Sun Wei-guo. 1988. Discovery of Chengjiang fauna at Meishucun, Jinning, Yunnan [in Chinese, with English summary]. *Acta Palaeontologica Sinica* 27:1-12.
- Howell, B. F. 1962. Worms, p. W144-W177. In R. C. Moore (ed.), *Treatise on Invertebrate Paleontology*, Part W, Miscellaneous. Geological Society of America and University of Kansas Press (New York and Lawrence).
- , and C. J. Stubblefield. 1950. A revision of the north Welsh *Conocoryphe viola* beds implying a Lower Cambrian age. *Geological Magazine* 87:1-16.
- Humm, H. J., and S. R. Wicks. 1980. *Introduction and Guide to the Marine Bluegreen Algae*. John Wiley & Sons (New York). 194 p.
- Jiang Zhiwen. 1982. Subclass Homopoda [in Chinese], p. 215. In Luo Huilin, Jiang Zhiwen, Wu Xiche, Song Xueliang, and Ouyang Lin, *The Sinian-Cambrian Boundary in Eastern Yunnan, China*. People's Publishing House, Yunnan.
- Johnson, J. H. 1966. A review of the Cambrian algae. *Colorado School of Mines, Quarterly* 61(1):1-162.
- Kozłowski, Roman. 1967. Sur certains fossiles ordoviciens à test organique. *Acta Palaeontologica Polonica* 12:99-130.
- Krishtofovich, A. N. 1953. Discovery of Lycopodiaceae in the Cambrian deposits of eastern Siberia [in Russian]. *Doklady Akademii Nauk SSSR* 91:1377-1379.
- Lendzion, Kazimiera. 1975. Fauna of the *Mobergella* Zone in the Polish Lower Cambrian. *Kwartalnik Geologiczny* 19:237-242.
- . 1977. *Cassubia*—a new generic name for *Pomerania* Lendzion, 1975. *Kwartalnik Geologiczny* 21:211.
- Liu Yi-ren. 1986. Middle Cambrian vermes in west Hunan [in Chinese, with English summary]. *Acta Palaeontologica Sinica* 25:336-337.
- Madsen, F. J. 1956. *Eldonia*, a Cambrian siphonophore—formerly interpreted as a holoturian [sic]. *Videnskabelige Meddelelser fra Dansk naturhistorisk Forening i Kobenhavn* 118:7-14.
- . 1957. On Walcott's supposed Cambrian holothurians. *Journal of Paleontology* 31:281-282.
- . 1962. The systematic position of the Middle Cambrian fossil *Eldonia*. *Meddelelser fra Dansk geologisk Forening* 15:87-89.
- Mansuy, H. 1912. Paléontologie. *Etude géologique du Yun-Nan Oriental*. *Memoires du Service Géologique de l'Indochine* 1(2):1-146.

- Matthew, G. F. 1899. Studies on Cambrian faunas, No. 3. Upper Cambrian fauna of Mount Stephen, British Columbia. The trilobites and worms. Transactions of the Royal Society of Canada, 2 series, 5:39-66.
- Mierzejewski, P. 1986. Ultrastructure, taxonomy and affinities of some Ordovician and Silurian organic microfossils. *Palaeontologia Polonica* 47:129-220.
- Missarzhevsky [Missarzhevskii], V. V. 1969. Description of hyolithids, gastropods, hyolithelminths, camenides, and forms of an obscure taxonomic position, p. 105-175. In M. E. Raaben (ed.), *The Tommotian Stage and the Cambrian lower boundary problem* [in Russian]. Transactions, Institute of Geology, Academy of Sciences of the USSR 206. [English translation published by Amerind Publishing Co., New Delhi, 1981.]
- P'an, K. 1957. On the discovery of Homopoda from South China. *Acta Palaeontologica Sinica* 5:523-526.
- Parker, B. C., and E. Y. Dawson. 1965. Non-calcareous marine algae from California Miocene deposits. *Nova Hedwigia Zeitschrift für Kryptogamenkunde* 10: 273-295.
- Paul, C. R. C., and A. B. Smith. 1984. The early radiation and phylogeny of echinoderms. *Biological Reviews* 59:443-481.
- Plotnick, R. E., and T. K. Baumiller. 1988. The pterygotid telson as a biological rudder. *Lethaia* 21:13-27.
- Prescott, G. W. 1968. *The Algae: A Review*. Houghton Mifflin Company (Boston). 436 p.
- Raymond, P. E. 1935. *Leandrothia* and other mid-Cambrian Arthropoda. Bulletin of the Museum of Comparative Zoology 76(6):205-230.
- Resser, C. E. 1938. Middle Cambrian fossils from Pend Oreille Lake, Idaho. *Smithsonian Miscellaneous Collections* 97(3):1-12.
- . 1939. The Spence Shale and its fauna. *Smithsonian Miscellaneous Collections* 97(12):1-29.
- , and Howell, B. F. 1938. Lower Cambrian *Olenellus* Zone of the Appalachians. *Geological Society of America, Bulletin* 49:195-248.
- Robison, R. A. 1976. Middle Cambrian biostratigraphy of the Great Basin. *Brigham Young University Geology Studies* 23(2):93-109.
- . 1984a. Cambrian Agnostida of North America and Greenland: Part I, Ptychagnostidae. University of Kansas Paleontological Contributions, Paper 109:1-59.
- . 1984b. New occurrences of the unusual trilobite *Naraoia* from the Cambrian of Idaho and Utah. *University of Kansas Paleontological Contributions, Paper* 112:1-8.
- . 1985. Affinities of *Aysheaia* (Onychophora), with description of a new Cambrian species. *Journal of Paleontology* 59:226-235.
- . 1986. Open-shelf Middle Cambrian biota of North America: an emerging perspective. *Geological Society of America, Abstracts with Programs* 18:177.
- Round, F. E. 1984. The systematics of the Chlorophyta: an historical review leading to some modern concepts [taxonomy of the Chlorophyta III], p. 1-27. In D. E. G. Irvine and D. M. John (eds.), *Systematics of the Green Algae*. Systematics Association Special Volume No. 27. Academic Press (London and Orlando).
- Ruedemann, Rudolph. 1909. Some marine algae from the Trenton Limestone of New York. *New York State Museum, Bulletin* 133:194-210.
- Satterthwait, D. F. 1976. Paleobiology and paleoecology of Middle Cambrian algae from western North America. Unpublished Ph.D. dissertation, University of California, Los Angeles. 121 p.
- Simonetta, A. M. 1964. Osservazioni sugli artropodi non trilobiti della "Burgess Shale" (Cambriano medio). III Contributo: I generi *Molaria*, *Habelia*, *Emeraldella*, *Parahabelia* (nov.), *Emeraldoides* (nov.). *Monitore Zoologico Italiano* 72:216-231.
- . 1970. Studies on non trilobite arthropods of the Burgess shale (Middle Cambrian). *Palaeontographica Italica* 66:35-45.
- , and Laura Delle Cave. 1975. The Cambrian non trilobite arthropods from the Burgess shale of British Columbia. A study of their comparative morphology, taxonomy [sic], and evolutionary significance. *Palaeontographica Italica* 69(n.s. 39):1-37.
- Smith, A. G., A. M. Hurley, and J. C. Briden. 1981. *Phanerozoic Paleogeographic World Maps*. Cambridge University Press (Cambridge). 102 p.
- Sokolov, B. S., and I. T. Zhuravleva (eds.). 1983. Lower Cambrian stage subdivision of Siberia. *Atlas of fossils* [in Russian]. Transactions, Institute of Geology, Academy of Sciences of the USSR 558:1-216.
- Sprinkle, James. 1973. Morphology and evolution of blastozoan echinoderms. *Museum of Comparative Zoology, Harvard University, Special Publication*, 283 p.
- Sun Wei-guo and Hou Xian-guang. 1987a. Early Cambrian medusae from Chengjiang, Yunnan, China [in Chinese, with English summary]. *Acta Palaeontologica Sinica* 26:257-271.
- and ———. 1987b. Early Cambrian worms from Chengjiang, Yunnan, China: *Maotianshanian* gen. nov. *Acta Palaeontologica Sinica* 26:299-305.
- Taylor, M. E., and H. E. Cook. 1976. Continental shelf and slope facies in the Upper Cambrian and lowest Ordovician of Nevada. *Brigham Young University Geology Studies* 23(2):181-214.
- Walcott, C. D. 1908. Mount Stephen rocks and fossils. *Canadian Alpine Journal* 1:232-248.
- . 1911a. Cambrian geology and paleontology II, no. 2—Middle Cambrian Merostomata. *Smithsonian Miscellaneous Collections* 57(2):17-40.
- . 1911b. Cambrian geology and paleontology II, no. 3—Middle Cambrian holothurians and medusae. *Smithsonian Miscellaneous Collections* 57(3):41-68.
- . 1911c. Cambrian geology and paleontology II, no. 5—Middle Cambrian annelids. *Smithsonian Miscellaneous Collections* 57(5):109-144.
- . 1912a. Cambrian geology and paleontology II, no. 6—Middle Cambrian Branchiopoda, Malacostraca, Trilobita, and Merostomata. *Smithsonian Miscellaneous Collections* 57(6):145-228.
- . 1912b. Cambrian of the Kicking Horse Valley, B.C. *Geological Survey of Canada, Report* 26: 188-191.
- . 1919. Cambrian geology and paleontology IV, no. 5—Middle Cambrian algae. *Smithsonian Miscellaneous Collections* 67(5):217-260.
- . 1931. Addenda to descriptions of Burgess shale fossils. *Smithsonian Miscellaneous Collections* 85(3): 1-46.
- Walton, J. 1923. On the structure of a Middle Cambrian alga from British Columbia (*Marpolia spissa* Walcott).

- Proceedings of the Cambridge Philosophical Society, Biological Sciences (Biological Reviews) 1(1):59-62.
- Werner, Bernhard. 1967. *Stephanoscyphus* Allman (Scyphozoa Coronatae), ein rezenter Vertreter der Conulata? *Palaeontologische Zeitschrift* 41:137-153.
- . 1973. New investigations on systematics and evolution of the class Scyphozoa and the phylum Cnidaria. *Publications of the Seto Marine Biological Laboratory* 20:35-61.
- . 1979. Coloniality in the Scyphozoa: Cnidaria, p. 81-103. In G. Larwood and B. P. Rosen (eds.), *Biology and systematics of colonial organisms*, Systematics Association Special Volume 11. Academic Press (London).
- Whiteaves, J. F. 1892. Description of a new genus and species of phyllocarid crustacean from the Middle Cambrian of Mount Stephen, British Columbia. *Canadian Record of Science* 5:205-208.
- Whitfield, R. P. 1894. On new forms of marine algae from the Trenton Limestone, with observations on *Bythograptus laxus* Hall. *American Museum of Natural History, Bulletin* 6:351-358.
- Whittington, H. B. 1977. The Middle Cambrian trilobite *Naraoia*, Burgess Shale, British Columbia. *Philosophical Transactions of the Royal Society of London (B)* 280: 409-443.
- . 1981. Rare arthropods from the Burgess shale, Middle Cambrian, British Columbia. *Philosophical Transactions of the Royal Society of London (B)* 292: 329-357.
- . 1985. *The Burgess Shale*. Yale University Press (New Haven). 151 p.
- , and D. E. G. Briggs. 1985. The largest Cambrian animal, *Anomalocaris*, Burgess shale, British Columbia. *Philosophical Transactions of the Royal Society of London (B)* 309:569-609.
- Zhang Wen-tang and Hou Xian-guang. 1985. Preliminary notes on the occurrence of the unusual trilobite *Naraoia* in Asia [in Chinese, with English summary]. *Acta Palaeontologica Sinica* 24:591-595.
- Zonenshain, L. P., M. I. Kuzmin, and M. V. Kononov. 1985. Absolute reconstructions of the Paleozoic oceans. *Earth and Planetary Science Letters* 74:103-116.